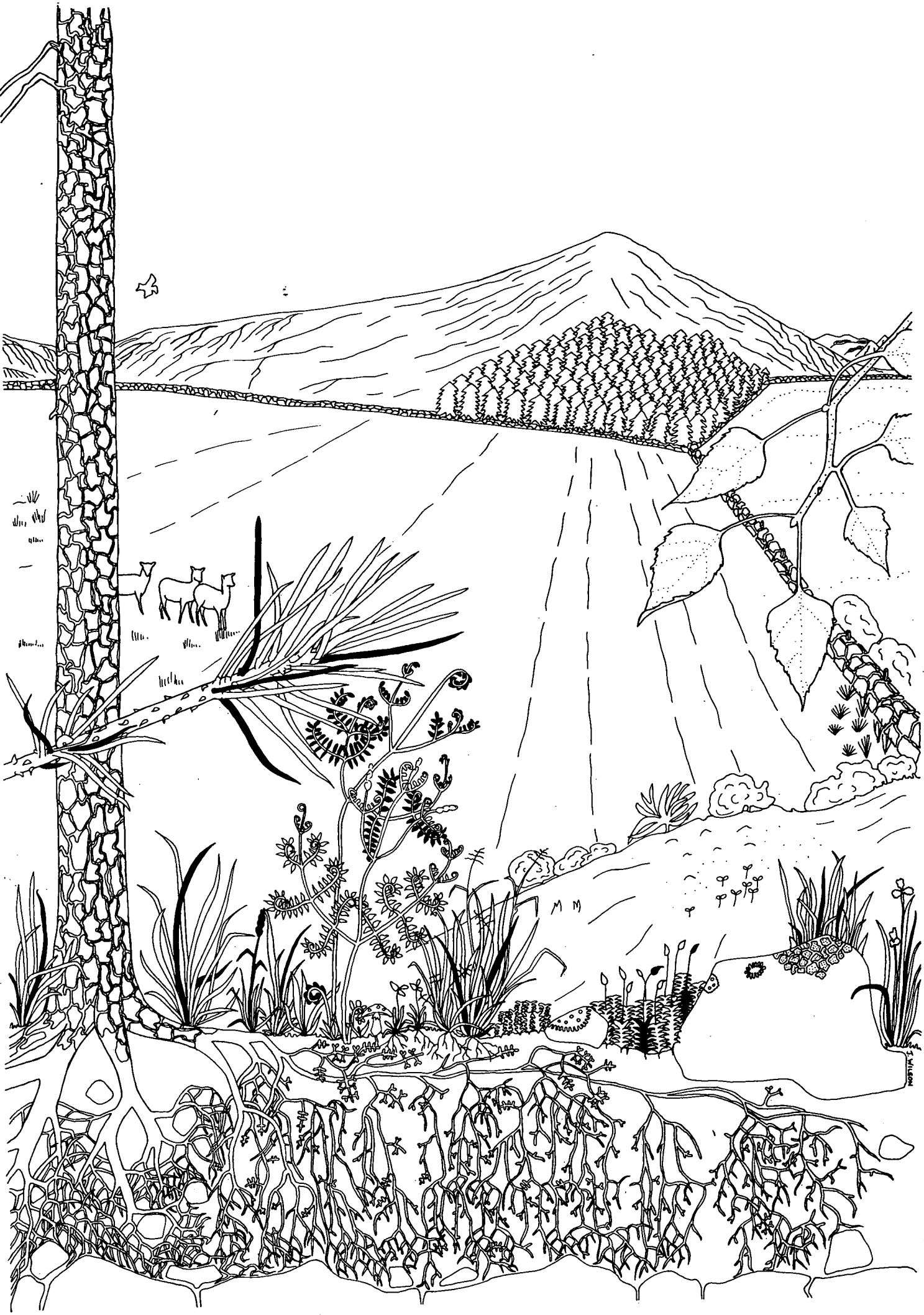
Forest and Woodland Ecology

Institute of Terrestrial Ecology
Natural Environment Research Council



Natural Environment Research Council

INSTITUTE OF TERRESTRIAL ECOLOGY

FOREST AND WOODLAND ECOLOGY

An account of research being done in ITE

ITE Symposium No. 8

Edited by

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The frontispiece was drawn by Dr. Julia Wilson, ITE, Edinburgh (Bush).

COVER PHOTOGRAPHS (photographers' names in brackets)

At the top: flower of *Triplochiton scleroxylon,* 'obeche' (K.A. Longman). Moving clockwise: *Cervus elaphus,* mature male red deer (B.W. Staines); Wychwood, Oxfordshire, type 4 in National Woodlands Classification (R.G.H. Bunce); excavated structural roots of *Picea sitchensis,* Sitka spruce, 16 years after planting in Dumfriesshire, Scotland (E.D. Ford); profile of a podzol (J. Miles); Sitka spruce plantation in Dumfriesshire, Scotland (E.D. Ford); *Accipiter nisus,* female sparrowhawk at nest with fledglings (R.S. Smith). Centre top: stomata of Scots pine, *Pinus sylvestris,* in unpolluted (left) and polluted (right) environments (A. Crossley). Centre bottom: mycorrhizal roots of *Betula pendula,* silver birch (S. Donaldson).

The Institute of Terrestrial Ecology (ITE) was established in 1973, from the former Nature Conservancy's research stations and staff, joined later by the Institute of Tree Biology and the Culture Centre of Algae and Protozoa. ITE contributes to, and draws upon, the collective knowledge of the fourteen sister institutes which make up the Natural Environment Research Council, spanning all environmental sciences.

The Institute studies the factors determining the structure, composition and processes of land and freshwater systems, and of individual plant and animal species. It is developing a sounder scientific basis for predicting and modelling environmental trends arising from natural or man-made change. The results of this research are available to those responsible for the protection, management and wise use of our natural resources.

Nearly half of the ITE's work is research commissioned by customers, such as the Nature Conservancy Council who require information for wildlife conservation, the Department of the Environment, the Department of Energy and the European Economic Community. The remainder is fundamental research supported by NERC.

ITE's expertise is widely used by international organisations in overseas projects and programmes of research.

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INTRODUCTION

Despite the extensive programme of planting started in the 1920s, Great Britain remains one of the least afforested of the developed countries. Its stock of trees, mainly coniferous (Figure 1 and Plate 27), which occupies about 7% of its land area, is unlikely to provide more than 10% of the country's requirement of timber and timber products.

Since the 1920s, attitudes have changed. The conservation, amenity and landscape interests of tree planters in the 18th and 19th centuries have come to the fore, but with a greater awareness of the indirect effects of afforestation, eg its effects on the quantity of water collected from different catchments, the effects of thinning and felling on soil erosion and water quality, and hence the development of fish and aquatic plants, etc. It cannot be denied that concern has been triggered by the scale of extant and projected planting programmes with sometimes dramatic changes in the mosaic of land uses, including the conservation of semi-natural woodlands. But do we fully appreciate the diversity of our natural woodlands? Do we know how to conserve them, recognising that all ecosystems are naturally subject to 'make or break'—they are dynamic? In considering the management of forests and woodlands, it is unquestionably desirable to adopt an integrated approach which takes into account their environments (atmospheric and edaphic), associated shrubs and herbs, harmful and beneficial microbes, pests and other animals (invertebrate and vertebrate), in addition to examining the biology of the trees themselves. Are we sufficiently alert to the fact that trees affect their environments (in addition to being affected by them) and those of associated plants and animals? Are the natural assemblages of plants in the uplands, where most of our coniferous plantings are being made, at risk? What of the assemblages in former coppicewoods? Can the effects of afforestation on populations of songbirds and their predators be predicted? By disrupting the former pattern of land uses, shouldn't we have expected that damage by deer and squirrels would be intensified?

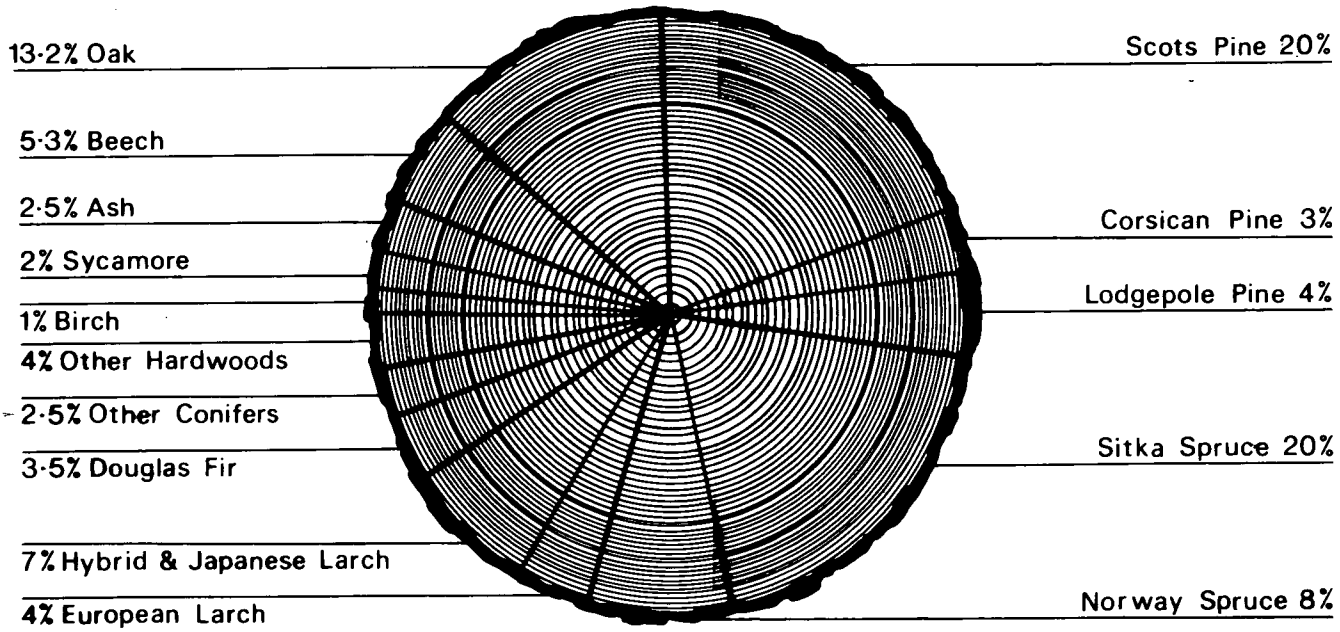

Fig. 1 *Proportion by area, of different tree species in woodland and afforested areas of Great Britain. (Locke, 1970).*

Foresters too frequently forget that they are dealing with the woody equivalents of ancient einkorn wheats. They are only now beginning to appreciate the full potential that exists in their chosen species which, compared with most modern agricultural crops, are extremely variable. Fundamental studies of the mechanisms and strategies of tree growth are now beginning to signal the way in which improvements may be sought. But in seeking these improvements shouldn't more attention be paid, than heretofore, to the exploitation of differences between species? It is hardly necessary to recount the damage done by the aggressive strains of *Ceratocystis ulmi*, the Dutch elm pathogen, to our vast stock of English elms which are thought to have been vegetatively propagated (naturally, as in hedgerows, and artificially) from relatively few introduced saplings. Even more recently we have been made painfully aware of the defoliating pine beauty

moth *(Panolis flammea)* which, while existing in 'harmony' with Scots pine *(Pinus sylvestris),* has done immense damage at a number of locations to plantings of the introduced lodgepole pine *(Pinus contorta).* Events of this sort suggest the need for concurrent studies of the ecology of semi-natural and man-made plantings. But could the upsurge of pine beauty moth have been predicted? By studying the phytophagous insects on the relatively few specimens of *Nothofagus obliqua* and *N. procera* (southern beeches from S. America) already growing in Britain, and on native trees (eg oaks and beeches) in the same family, the Fagaceae, will we be able to ward off danger if species of *Nothofagus* are to be grown extensively? At the very least, we should have an awareness (Plates 1, 2 and 3).

Unlike agriculturists who have switched their crop plants from one climate zone to another, foresters have been more cautious. However, there are signs of a greater degree of speculation with the growth of *Nothofagus* spp and *Pinus radiata* in parts of Britain much further from the equator than their native habitats. To an extent, these transfers can be aided by fundamental studies of tree biology. What restricts their growth, and can these constraints, eg frost sensitivity, be overcome by selection, by silvicultural practices, etc? For that matter, it seems desirable to re-assess existing practices, remembering that the attributes required in a tree after planting, but before canopy closure, are different from those when subject to severe competition after canopy closure. Have we been bold enough in our approaches to the problem of windthrow? Could we learn more from the architecture of trees that have successfully occupied exposed habitats?

In the late 1960s, most trees in woodlands and afforested parts of Great Britain were coniferous (Figure 1). Since that time, the proportions of Sitka spruce and lodgepole pine have increased, Sitka spruce now forming at least 35% of coniferous plantings compared with 27% in 1970: the proportion of lodgepole pine has gone from 5.5% to more than 8.0%. However, against these figures should be set the enormous numbers of trees growing ouside the confines of woods and forests—a group including many native, and a considerable variety of introduced, trees not usually included in the forester's repertoire. This resource, like that of forests and woods, serves many purposes, eg it provides amenity and niches for wildlife: if properly sustained it could provide fuel, and possibly veneer timber.

In seeking solutions to many of the problems that have been posed, the Natural Environment Research Council, with its charter remit for long-term forest and woodland research, has (i) awarded grants and studentships to staff and students at Universities and Polytechnics and (ii) supported a considerable array of projects at some of its Institutes. Projects done at the Institute of Terrestrial Ecology are discussed in this volume. They reflect the Institute's concern for tropical forestry, notably the conservation of *Triplochiton scleroxylon,* a valuable West African tree whose natural stands have been selectively and seriously depleted. In this instance, research has centred on the phenomenon of phase change and its influence on the rooting of cuttings and flower induction—problems also fundamental to forestry elsewhere in the world. Another series of projects of topical international concern relates to the aerodynamic and plant factors controlling the removal of atmospheric pollutants, gaseous and particulate—a subject akin to the study of carbon dioxide and water vapour fluxes which forms an integral part of the programme of tree biology.

While the Natural Environment Research Council finances most of the work done at the Institute of Terrestrial Ecology from funds received from the Department of Education and Science, some of the work described in this volume was commissioned by the Department of the Environment, the European Economic Community, the Nature Conservancy Council and the Overseas Development Administration. Members of the Institute of Terrestrial Ecology wish to acknowledge the help and interest of those organisations, and also the valued co-operation of colleagues in the Forestry Commission, the Red Deer Commission and many university Departments.

The help received from Mr R. Medler who prepared the figures is greatly appreciated. Mr Medler, a cartography student at the Luton College of Higher Education, worked at Monks Wood during a period of 'industrial' training.

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Nature of tree and woodland resources

1. BRITISH WOODLANDS IN AN EUROPEAN CONTEXT

R.G.H. BUNCE

Ecologists concerned with British and continental European woodlands have tended to go their own distinctive ways, although there are notable exceptions. Klotzli (1970), using the Braun-Blanquet system, made a comparative study of British and continental woodlands using published data, as did Rubner and Reinhold (1953) who included a chapter on British woodlands.

In general, one can only agree with Dierschke (1971) who indicated that British vegetation is amongst the least known in Europe. Although Braun-Blanquet and Tuxen used the former's system of phytosociological classification when describing woodlands in Ireland in 1952, British interest in this system owes most to a series of papers published by Poore in 1955 (*a, b* and *c*). Recently Birse and Robertson (1976) have made a study of plant communities in southern Scotland. Considerable difficulties are encountered when attempting to fit British woodlands into the system, in part because of inherent differences in species combinations, but also because of variations in interpretation of the classification by continental authors. For example, Kiellund-Lund (1973) describes associations in Scandinavia, Westhoff and Den Held (1969) in Holland, Hartman and Jahn (1967) in mountain areas north of the Alps, and Durin *et al.* (1968) in northern France, but the presentations differ markedly in the degree of separation of the classes. These variations appear to be largely in response to the particular vegetation present in the areas concerned—thus Kiellund-Lund divides the extensive Vaccinio-picetea forests of Scandinavia whereas Durin *et al.* divide the Quercetea roboripetrae forests of the Atlantic margins. Despite various attempts, notably that by Lohmeyer *et al.* (1962), the differences between the various associations proposed for woodlands need further study, not only by appropriate data collected from British woodlands but also to enable their vegetation to be accurately assessed using the system.

British and continental woodlands differ greatly in scale, the former, with complex management histories, invariably being fragmented. As a result many non-woodland plants are found within British woods. This effect has its greatest expression in the open woods of the north-west of Scotland, where the varied geology and heavy rainfall further complicate the situation. In contrast, in much of lowland Europe, habitats, with less variable geology, are more uniform, a comparable degree of complexity only being found in the Alps. This generalisation was confirmed when the variation within a small sample of continental and British woodlands was assessed. Nonetheless a few types of vegetation are more variable on the continent than in Britain.

1. General comparisons

When surveying native British woodlands, Bunce and Shaw (1972) developed a system of classification with 32 habitat types (Figure 2). At one extreme, in the level land of eastern England, the climate is markedly continental, soils are invariably deep and calcareous, and the woodlands are set in a matrix of arable agriculture. Canopy species are mainly *Fraxinus excelsior, Ulmus* spp and *Acer campestre* with *Mercurialis perennis* and *Rubus* spp forming the ground flora (types 1-8). In similar climatic conditions, but on soils with small amounts of calcium, *Quercus petraea* and *Betula* spp predominate in the usually dense canopy, *Mercurialis perennis* being replaced by *Pteridium aquilinum* in the ground layer (types 17-24). In contrast in very wet habitats, but still lowland, *Salix* spp and *Alnus glutinosa* are the predominant canopy species with *Iris pseudacorus* and *Phalaris arundinacea* in the ground flora (types 13-16). In habitats in northern Scotland with extremely small amounts of nutrients and a sub-boreal type of climate (types 27-28), *Pinus sylvestris* is the major species with *Calluna vulgaris* and *Vaccinium vitis-idaea* typically among ground flora species. In other less extreme situations still subject to a markedly oceanic climate and with shallow acidic and often rocky soils, woodlands are characterized by *Quercus petraea* and *Betula* spp with *Deschampsia flexuosa* and *Vaccinium myrtillis* occurring distinctively on the ground (types 25-26 and 29-32). These types have now been compared somewhat tentatively with the Braun-Blanquet system, mainly based on the associations described by Kiellund-Lund (1973) (Plates 4, 5 and 26).

Types 25, 26, 27-30 with *Quercus petraea* and *Betula* spp have their counterparts in Scandinavia and western Europe, the woodlands often having similar structures. Most of the species in northern continental woodlands occur in Britain, although

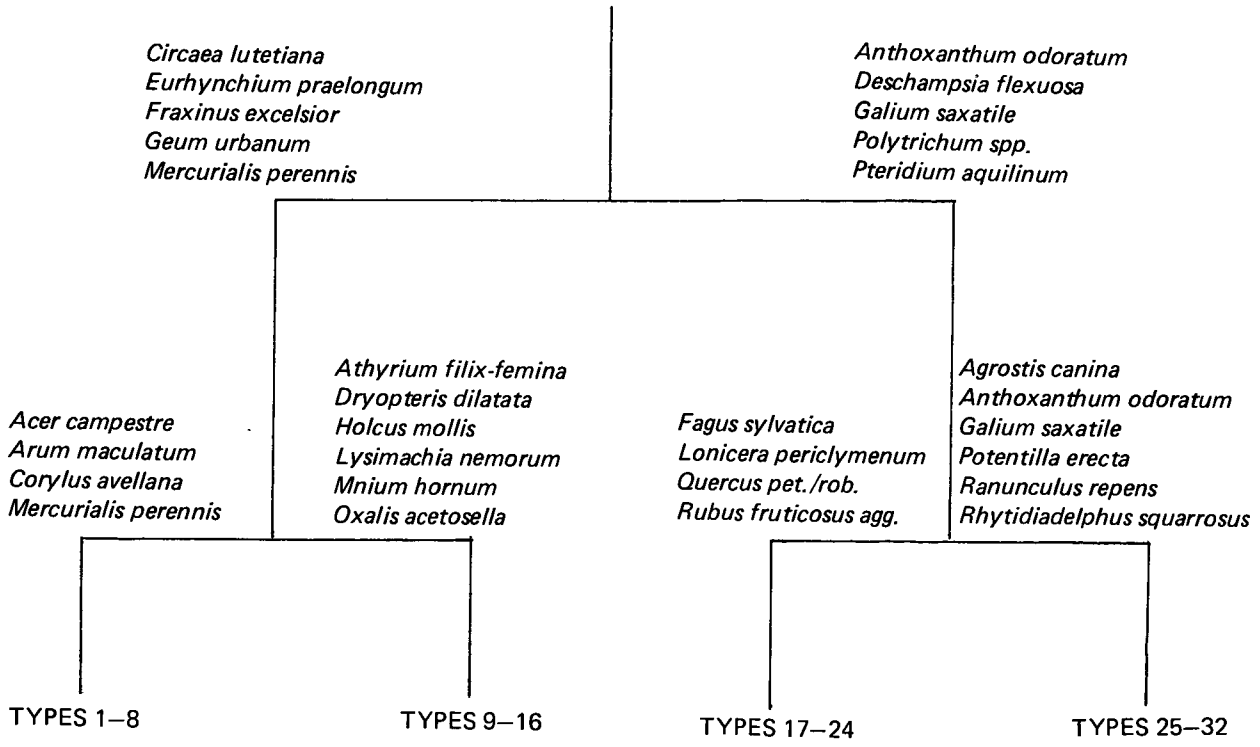

Fig. 2 *The first two dichotomies of an indicator species analysis (Hill* et al., *1975) of British woodland vegetation. The species at each dichotomy are identified by the computer as the most useful to separate the samples into 2 groups. The data were obtained from 1648 plots, each 200 m², sited at random at 16 locations in each of 103 sites taken as representative of the range of variation within British woodland vegetation.*

progressively, as one moves away from the Atlantic influence towards central and eastern Europe, species such as *Sambucus racemosa* and *Hepatica nobilis* with continental distributions appear at the expense of Atlantic species such as *Endymion non-scriptus* and *Galium saxatile.* It is not until the Alps are reached that the main canopy species alter with extensive forests of *Picea abies,* although *Fagus sylvatica* and *Ulmus glabra* are still important dominants locally. There are, however, species-assemblages present in continental alpine woodland that have no direct parallel with those in Britain, eg the species associated with *Alnus incana* on talus slopes. Similarly the majority of species in the Mediterranean zone—eg *Fraxinus ornus, Quercus pubescens* and *Cistus* spp.—are not represented in Britain nor are *Acer tartaricum* and *Fagus orientalis* and many other species which are found in the eastern Mediterranean. In eastern Europe, the main link with assemblages found in Britain is lost in eastern Poland with the disappearance of *Fagus sylvatica.*

In general, the woodlands of much of Scandinavia and of mainland western Europe have much in common with those in Britain. There is a progressive replacement of species to the south and east, but some similarities can be discerned until the Alps and the Mediterranean are reached. As in Britain, large scale differences are determined by climate, with local differences being mainly attributable to soil type.

2. Numerical comparisons

In 1974 a visit was made to Belgium and northern France and data were collected from 75 woodland plots (Figure 3) using the method described by Bunce and Shaw (1972). These were added to data from 3 plots drawn at random from each of the 32 woodland types in Britain, so that detailed comparisons could be made by (1) indicator species analysis (Hill *et al.,* 1975) and (2) reciprocal averaging ordination (Hill, 1973).

Accepting that the range of types was probably incompletely recorded, it is nevertheless of interest to find that 17 of the 32 classes identified in Britain were represented in the sample from Belgium and northern France. There were several notable absentees including the western acid oakwood (types 25 and 16), the assemblages in extremely wet situations and those typical of extreme upland situations (28 and 29). The absence of lowland calcareous woodland types is attributed to defective sampling but even so Belgium clearly has a greater frequency of basiphilous types. The major separations in the indicator species analysis of data (Figure 4) from Belgian and northern French woodlands are, in all but one instance, dependent upon the same species as in the comparable analysis of British woodlands. Some groups are predominantly British eg Group 1, whereas others are mainly composed of continental plots eg Group 6, reflecting differences in

Fig. 3 *Geographical location of sample woodland sites.*

the balance between the species combinations in the 2 areas.

The same picture emerges from the reciprocal averaging ordination (Figure 5) where data from the Belgian and French woodlands overlap to a very considerable extent with those from British woodlands. To the extreme right of Figure 5 are 2 groups of plots, one from the Ardennes and the other from northern Scotland, the 2 being separated by the proportion of moisture loving species. There is a considerable concentration of continental woodlands in the bottom centre of Figure 5 emphasizing the frequency of dry acidic sample plots covered and so contrasting with the absence of Belgian and French woodlands in very wet locations (see top of Figure 5).

3. Discussion

The analyses made up to this time, albeit on a restricted number of continental samples, serve to stress affinities with British counterparts, and

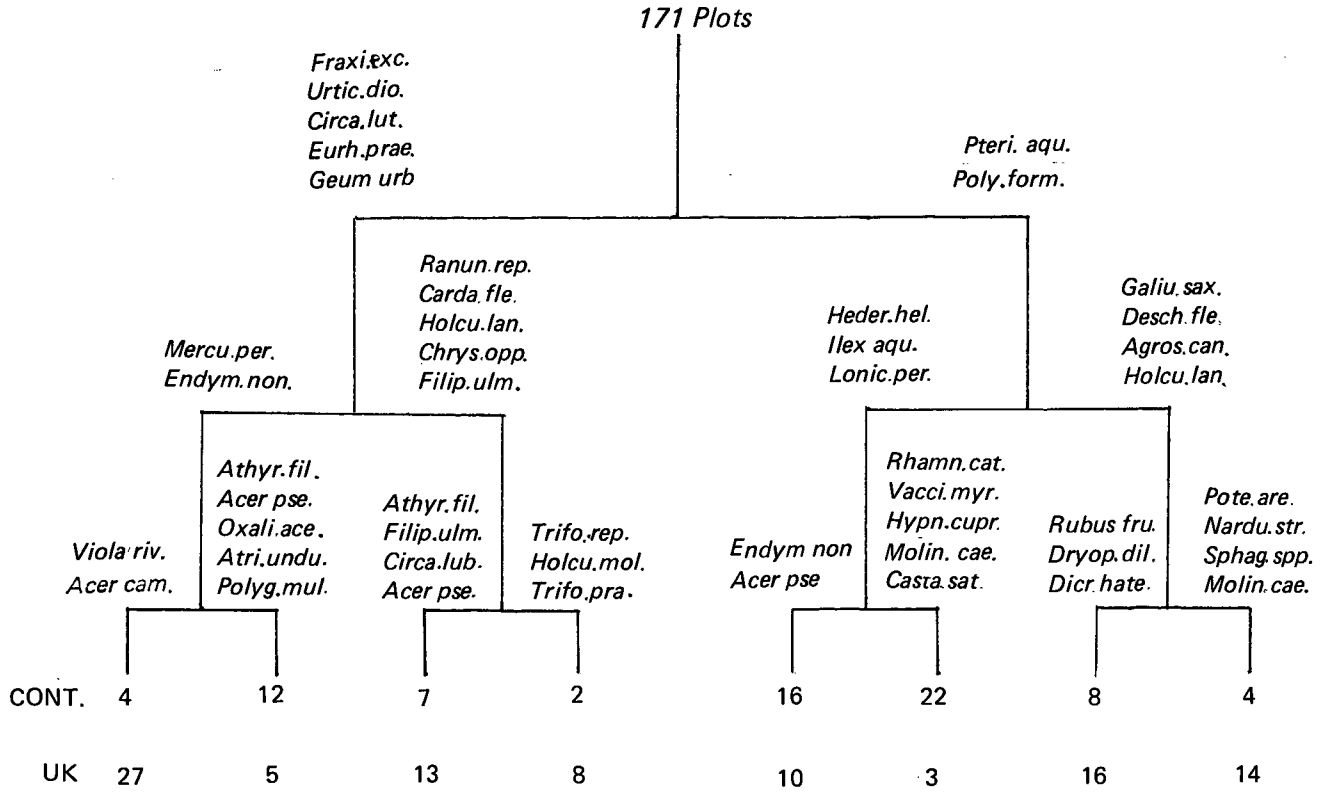

Fig. 4 *Hierarchy of an indicator species analysis (Hill* et al., *1975) of combined data from 75 plots recorded in Belgium and northern France and from 3 plots drawn at random from each of 32 woodland types in Britain. The numbers at the base of the hierarchy refer to the continental or British origin of the plots of each group.*

suggest that it would be profitable to obtain an extended range of data. Within Britain the analysis has highlighted the existence of 32 types of woodlands, whose existence should be recognised when selecting a typical range for ecological studies.

The selection of sites for nature conservation is to some considerable extent based on "representativeness' which, in the Nature Conservation Review, is essentially concerned with vegetation assemblages. If the relation of British to continental European woodlands were known, it is possible that conservation priorities within Britain would be changed.

The classification of vegetation should be regarded as a means to an end and not an end in itself. It highlights affinities and suggests assemblages for synecological studies. Perhaps at the present time when attention is being switched to woody perennials, trees, as renewable energy crops, the classification can point to areas in Britain where satisfactory energy crops might be grown.

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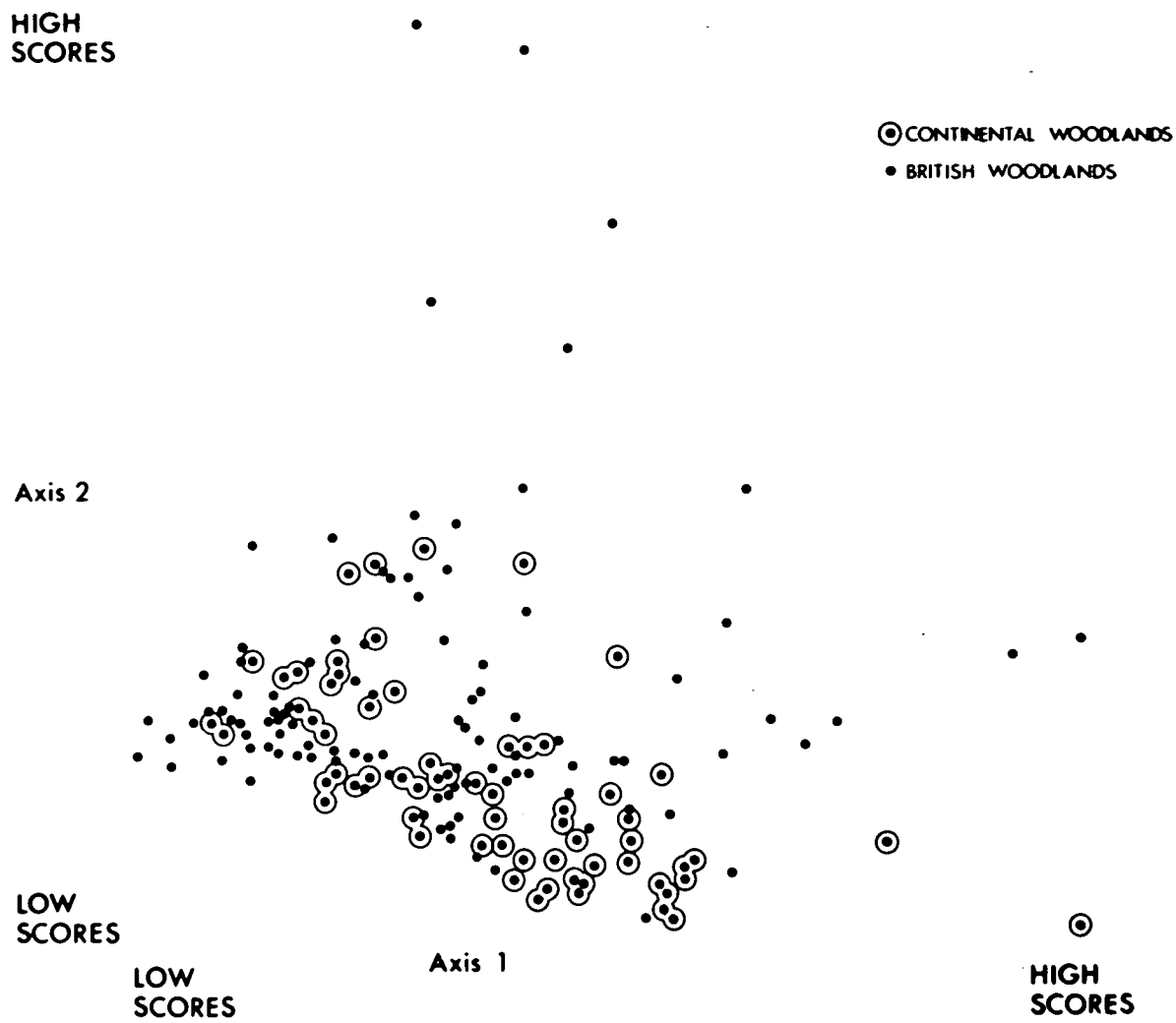

Fig. 5 *Scatter diagram of each reciprocal averaging ordination (Hill, 1973) showing the overlap between continental and British woodlands, reflecting the overall relationships of their composition.*

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2. SCOTTISH DECIDUOUS WOODLANDS: A CAUSE FOR CONCERN?

T.W. PARR

The management of a resource can only be effectively achieved if it is related to a detailed knowledge of the current status of the resource. For woodlands it is necessary to have information about quantity, distribution and composition. From 1976 to 1978 information of this sort was obtained for deciduous woodlands in Scotland, the data being incorporated into a computer data bank of a kind enabling easy access and facilitating detailed ecological analyses. In the hope of assessing whether changes had occurred, attempts were made to reconcile these data with those from an earlier survey done by the Forestry Commission from 1947 to 1948.

1. Survey method

In searching the 7th series 1" ordnance survey maps, all woods containing a broadleaf symbol (effectively those of 5 hectares or over) were recorded together with details of grid reference, name, district, location (and county) and altitude, Between summer 1976 and autumn 1978, field visits were made to confirm the continuing existence of the different woods and, if they existed, to determine the composition of their canopies. Twenty-one tree species or species groups were recorded (Table 1); the contribution (% cover) of each species or species group to total cover was estimated by eye having visited as many vantage points as feasible. Where more than 50% of the canopy was attributable to conifers, the entry was deleted from the inventory as also happened if less than 50% of the site had tree cover. Woods which had been underplanted with conifers or clear felled were also omitted.

2. Inventory

Data for 3,631 of 3,747 woods have so far been put in the data bank (Table 1). The percentage of the total land area covered by deciduous woods varies from 0.2% in Selkirkshire to 2.5% in Stirling, with counties in the lowland areas tending to have a larger woodland cover. Of the total of 66,000 ha of woodland, 46% is occupied by birch, this species group's widespread distribution particularly in the northerly counties reflecting its dominance in (1) early successional scrub woodlands and (2) climax birch woodlands occurring at either high altitudes (between 800 ft (250 m) and 2000 ft (600 m)), or on poor thin soils where oak and pine cannot thrive.

The straightforward county summaries can be supported by more detailed computer printed maps, on which are plotted figures indicating numbers of woods in a rectangular area of c. 45 km^2 in which a particular species is dominant (i.e. the species with the largest % cover). Beech dominates many woods at the northern fringe of the lowlands, including the Central valley, where it was planted in policy woods (Figure 6).

3. Assessment of change

Comparisons of the 1947-49 Forestry Commission (FC) census of woodlands and the survey described in this article suggest, if methodological differences are ignored, that the area of deciduous woodland in Scotland has decreased by 56% with very small losses of 1% in some counties (Caithness and Kinross) and very large losses, 80%, in others, notably Kincardine and Selkirk (Figure 7). Despite these variations, there are no distinct regional patterns excepting possibly smaller losses in the most northerly counties.

The species composition of Scottish woods has changed very little during the last 30 years, the most notable change being a decrease in the cover provided by beech, from 14% to 8%. It therefore seems that the loss of deciduous woodland, in part attributable to conversion to conifers, has affected all types more or less similarly.

Although the direct comparison of Forestry Commission and ITE surveys indicates the broad direction of change, it is necessary to be aware of their many methodological differences before reaching precise conclusions. Thus, in contrast to the current ITE survey, the FC census was based on 6" ordnance survey maps; it included woods between 2 and 5 ha in addition to those larger than 5 ha, and areas of mixed woodland were divided into homogenous stands which were then treated as separate units. To assess the significance of these differences in relation to assessments of rates of change, the details for Selkirkshire were considered in greater depth.

4. Selkirk

The map search in 1977 suggested that there were 17 woods, 5 ha or more, in Selkirkshire, of which 6 were deleted after making ground checks; the remaining 11 woods covered an area of 129 ha. The 1947 FC census identified a total of 649 ha of deciduous woods (including areas of mixed forest and scrub), suggesting a woodland decrease

$$\frac{(649 - 129) \times 100}{649}$$

TABLE 1 Inventory of deciduous woods in Scotland, with specific reference to tree species or species groups forming more than 1% of canopy.

Species codings are: SY = sycamore, EL = elm, BE = beech, AS = ash, EX = exotics, LI = lime, SP = Scots pine, OA = oak, CH = cherry, HA = hawthorn, WI = willow, AL = alder, HZ = hazel, AP = aspen, RO = rowan, BI = birch. Contributions of holly, hornbeam, blackthorn, whitebeam and yew to woodland canopies never exceeded 1%.

County	Areas of deciduous woodland (ha)	Areas of woodland as % of area of county	SY	EL	BE	AS	EX	LI	SP	OA	CH	HA	WI	AL	HZ	AP	RO	BI
Sutherland	2900	0.6	1	0	1	1	3	0	2	4	0	0	2	6	2	1	3	74
Caithness	500	0.3	14	5	15	9	8	0	1	0	0	0	0	1	1	1	2	43
Ross	4020	0.6	1	0	4	1	4	0	7	9	0	0	1	2	2	0	2	67
Inverness*	10100	0.9	0	0	1	2	4	0	9	12	0	0	0	2	1	0	1	68
Nairn	630	1.5	1	0	11	6	10	0	2	8	0	0	0	0	0	0	0	62
Moray	1910	1.6	1	0	5	0	9	0	1	3	0	0	0	0	0	0	0	81
Banff	1250	0.8	4	2	9	5	14	1	11	5	0	0	0	3	0	0	1	45
Aberdeen*	2860	0.6	3	1	10	3	12	0	2	5	0	0	1	3	0	0	0	60
Kincardine*	440	0.4	3	3	9	3	7	0	5	4	0	0	2	1	0	0	1	62
Angus*	1360	0.6	3	4	23	3	9	0	4	8	0	0	2	1	0	0	0	43
Argyll	10190	1.3	3	1	4	4	6	0	1	36	0	0	1	2	2	0	1	39
Perth	7230	1.1	2	3	7	4	13	0	1	23	0	0	0	2	0	0	0	44
Stirling*	2960	2.5	10	4	8	5	7	0	2	31	0	0	1	2	0	0	0	30
Kinross	300	1.4	4	2	15	2	6	1	1	5	0	0	0	0	0	0	0	64
Dunbarton	1440	2.3	7	1	5	5	5	0	3	41	0	0	0	4	1	0	0	28
Clackmannan	280	2.0	7	6	12	10	13	0	3	5	0	0	1	4	0	0	0	39
Fife*	1400	1.1	16	9	14	7	11	1	2	9	0	0	1	1	0	0	0	29
Renfrew	770	1.3	21	4	19	8	7	1	1	8	0	0	1	1	0	0	0	29
Bute*	670	1.2	5	1	15	4	6	2	1	10	0	0	1	7	1	0	0	47
Ayr	2480	0.8	11	5	16	12	8	1	1	12	0	0	3	3	0	0	0	28
Lanark	2390	1.0	11	7	17	7	9	3	3	8	0	1	3	2	0	0	0	29
W. Lothian	350	1.1	15	19	14	6	9	3	3	14	1	1	2	0	0	0	0	13
Midlothian	1410	1.5	14	10	18	9	21	1	3	13	0	0	0	0	0	0	0	11
E. Lothian	1030	1.5	15	8	12	11	15	3	8	13	0	0	0	0	0	0	0	15
Peebles	350	0.4	6	7	17	8	18	2	12	7	0	0	1	1	2	0	0	19
Berwick*	920	0.8	18	6	17	6	9	1	4	19	0	0	0	0	0	0	0	20
Selkirk	130	0.2	5	11	9	21	15	1	2	21	0	0	0	1	0	0	0	14
Roxburgh*	730	0.4	10	12	17	7	13	1	4	25	1	0	0	1	0	0	0	9
Wigtown	1180	0.9	17	5	18	10	10	0	1	14	0	0	3	3	0	0	1	18
Kirkcudbright	1860	0.8	8	2	9	8	5	0	0	37	0	0	2	2	0	0	0	27
Dumfries	1990	0.7	5	3	14	10	7	0	1	30	0	0	0	3	0	0	0	27
Totals	66030																	
Means		0.9	5	3	8	5	8	0	3	18	0	0	1	2	1	0	1	45

Asterisk indicates that survey was less than 98% complete.

of 80% during the last 30 years. To assess the accuracy of this direct comparison, woods (or groups of stands) in the FC census with areas of 5 ha or over, and with a deciduous tree cover of at least 50%, were identified. There were 26 woods amounting to 473 ha. The balance (649-473) of 176 ha (27% of the total) consisted of either small areas of deciduous woods less than 5 ha, or small areas of deciduous trees in larger blocks of coniferous woods.

Of the 26 woods 14, with a total area of 133 ha (or 20% of total), were not included in the 1977 survey because, although individually larger than 5 ha, they tended to be long and thin, eg riverine woods, roadside woods and shelter belts, and of insufficient width to contain a broadleaf symbol on 1" ordnance survey maps.

Thus, of the 649 ha of broadleaf woodland identified by the FC in 1947, 27% were in woods of less than 5 ha and 20% were excluded in the 1977 survey because small scale maps were used. With their omission, the balance (649-176-133) of 340 ha recorded in 1947/49 should be compared with 129 ha confirmed in 1976/78. The deciduous

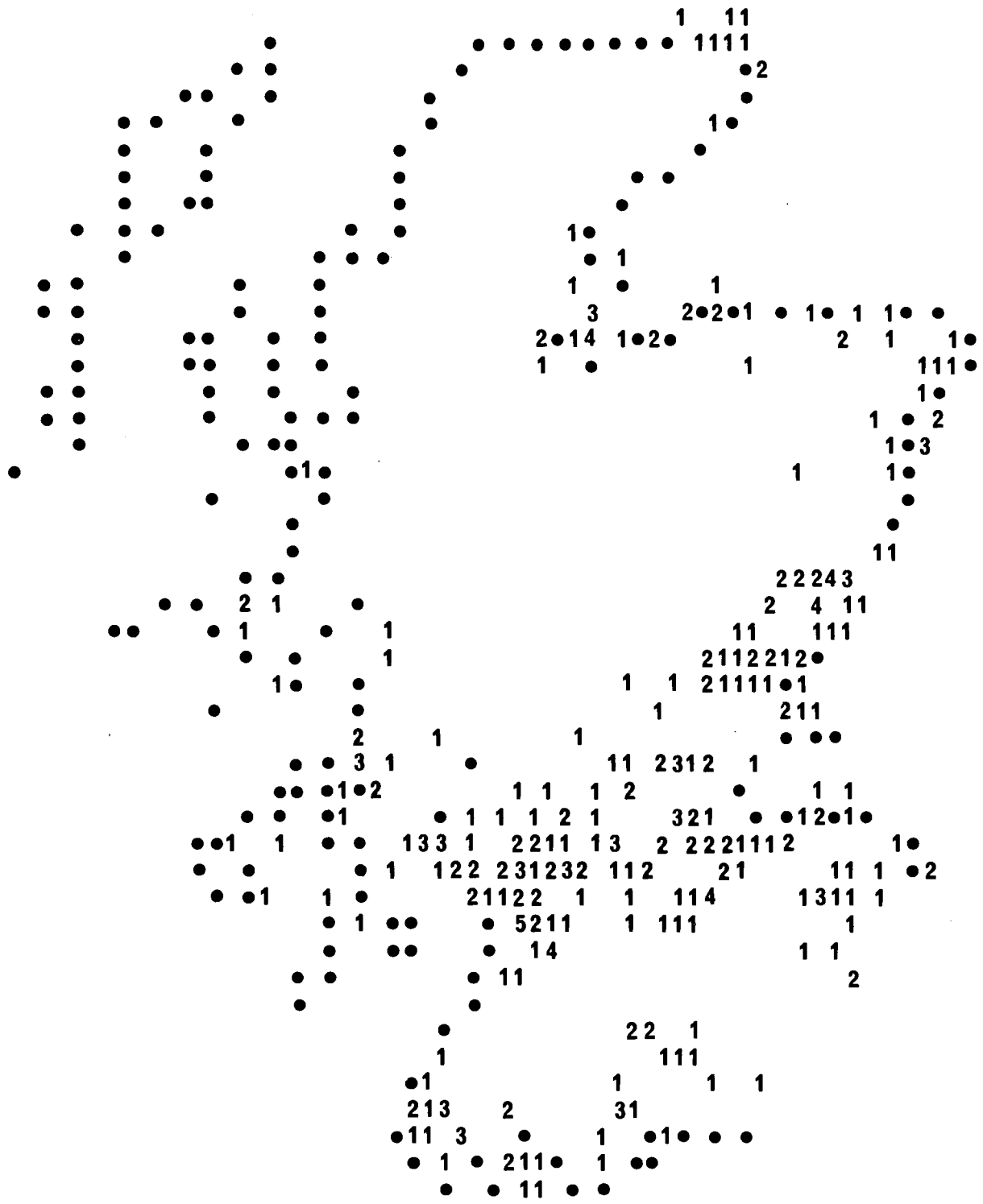

Fig. 6 *Copy of a computer produced map of Scotland (coastline shown by dots) showing the distribution of woods in which beech is dominant. Each figure represents the number of woods in a rectangular area of approximately 45 km².*

woodland cover of Selkirkshire seems therefore to have decreased by 62% during the last 30 years, a figure comparing with 80% calculated from unadjusted data. This loss can be attributed to (i) the clearance and replacement of birch scrub by conifers and (ii) the underplanting of deciduous trees, which remain locally abundant, with conifers. Because the effects of the latter are neither instantaneous nor dramatic, the gradual conversion from deciduous to coniferous may go unnoticed.

5. Discussion

Remembering that it is by no means a typical county, it would be foolish to extrapolate from Selkirkshire to obtain 'corrected' estimates of woodland decreases for the remainder of Scotland. In addition to having the smallest area of deciduous woodland, it has lost a greater proportion than any other county except Kincardine. Furthermore it is expected that differences in woodland configurations may affect the outcome of compari-

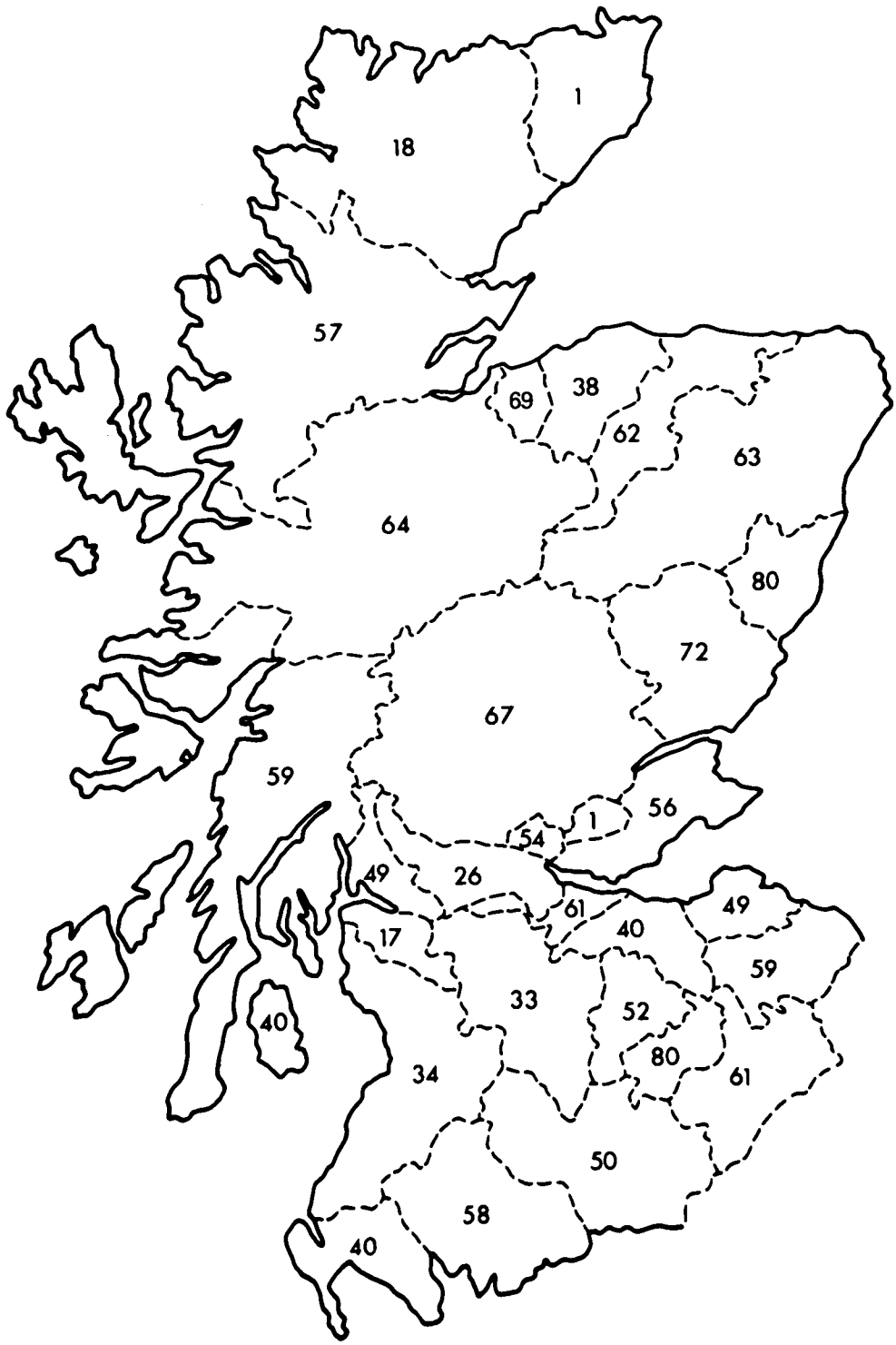

Fig. 7 *Map of Scottish counties showing the estimated decreases (%) in woodland cover when ignoring methodological differences between the Forestry Commission's 1947/49 census of woodlands and ITE's survey made during 1976 and 1978 (see text for interpretation).*

sons between the FC and ITE surveys. Nonetheless, the 1976/78 inventory indicates that the deciduous woodland resource in Scotland has been significantly decreased during the last 3 decades. There is no reason to be complacent if the already small area of deciduous woodland, less than 1% of the area of Scotland, is to be sustained.

3. TREES IN TOWN AND COUNTRY

J.E.G. GOOD and R.C. MUNRO

Compared with most other European countries, the United Kingdom lacks forests, but is well endowed with amenity trees, a result of large scale clearances over many centuries being offset to some extent by small scale plantings for shelter, estate amenity and the delimitation of fields (Good, 1976). However, recent fundamental changes in agriculture, with the amalgamation of small fields into larger units, have resulted in the loss of hedgerows and, in many instances, the removal or neglect of small areas of woodland (Westmacott & Worthington, 1974). Inevitably, public interest has been aroused and to some extent fostered by the current devastating attacks of the aggressive strain of *Ceratocystis ulmi* (Buism.) Moreau, the fungus causing Dutch elm disease (Brasier & Gibbs, 1973). How should our resource of amenity trees be sustained? What problems have to be overcome in relation to site conditions, species selection, maintenance, vandalism and the provision of planting stocks by the horticultural trade? Before these questions can be answered, we need a detailed understanding of the nature of the resource, its size and composition by age and species. So far, detailed surveys have been limited to the Lothian region.

1. Survey of the Lothian region

The survey was done in 2 parts (a) the city of Edinburgh during 1972 (Last *et al.*, 1976) and (b) the remainder of the Lothian region, including the districts of East, Mid and West Lothian, in 1974-75 (Good *et al.*, 1978). Forestry Commission woodlands, grant-aided woodlands, worked coppice, commercial orchards and hardy-stock nurseries were omitted.

1.1 Site selection

The city of Edinburgh was considered in 2 parts, residential and non-residential.

(i) Residential—From a cursory survey, it was obvious that the distribution of trees was overwhelmingly influenced by social considerations and was not strongly related to traditional site factors such as soil type and aspect. As a result, residential areas were divided by owner-occupancy into 4 categories using data from the 1966 census (HMSO 1968) *viz* areas with 0-25, 26-50, 51-75, 76-100% owner-occupiers (Waugh, 1973). Twelve localities were selected at random within each of the 4 occupancy categories, each locality, usually delimited by roads, being not less than 2 ha and not more than 7.

(ii) Non-residential—Excepting cemeteries, private parks and public utilities, non-residential areas of Edinburgh were identified on 1/24000 scale aerial photographs (Meridian Air Maps, 1971), measured and allocated to one of 5 classes: (1) tree-lined parks with trees restricted to the perimeter and/or verges alongside roads, (2) open parks where the few trees were small, (3) golf courses where the few trees, like those in open parks, were small, (4) parklands where trees are open-grown and scattered, (5) woods where the many trees create a woodland character. In total, 21% of the 929 "non-residential" ha was observed.

East, Mid- and West Lothian. These districts were divided into urban and rural areas, the latter being subdivided into upland and lowland, above and below the 500 ft (160 m) contour. A sampling system based on conveniently delineated sectors in urban areas (burghs), and 1 km National Grid squares in rural areas was used. Total enumerations were made of randomly selected urban sectors, whereas, in rural areas, each selected 1 km square was divided into 100 strips each 20 m wide, 50 being orientated N/S and the other 50 in an E/W direction. Two of these strips were chosen at random for survey, within each square, giving a 4% coverage.

1.2 Enumeration

Trees were defined as perennial woody plants with main stems taller than 1.8 m (6 ft). They were usually categorised into species, but, in some instances, to species-aggregates with 0.2% remaining unclassified. Diameters at breast height (1.3 m) were also recorded. In the Edinburgh survey, a utility assessment was made of those stems exceeding 30 cm, using 3 categories, non-utilisable, if less than 1.8 m of clear stem, if stem form was very bad (fluted, twisted, buttressed...), if evidence of microbial decay..., utilisable, if 1.8 m or more of clear stem without major defects of the type described for non-utilisable, good quality, if 1.8 m of clear stem without defects.

1.3 The resource

The Lothians are not thought to be heavily endowed with amenity trees compared with other parts of Britain (Locke, 1970), but, even so, and allowing for the sizeable statistical error, the total of 6.7 million trees (± 27%) represents a very considerable resource, equivalent to about 10 trees per head of population and 36 trees ha^{-1} (Table 2).

TABLE 2 Distribution of amenity trees in the Lothian region (1972-75) (Good *et al.*, 1978)

Land categories	Total area km^2	Area sampled km^2	No. of trees in samples	Estimated total no. of trees (Millions)	Mean no. per ha
D. Burghs (A)	232	11.2	73000	1.4 ± 0.37	59
Lowland rural (B)	741	4.2	17000	3.2 ± 0.89	43
Upland rural (C)	904	4.5	10000	2.1 ± 0.59	24
Region (A+B+C)	1877	19.8	100000	6.7 ± 1.84	36

Amenity trees were found to be unevenly distributed, greater concentrations (trees/ha) occurring in towns than in rural areas, where the lowlands are predominantly arable and the uplands, sheepwalk. On average, broadleaved trees outnumbered coniferous trees by a factor of 2.5. As might be expected the contrast was greater in the burghs (84% broadleaved: 16% coniferous) than in upland rural areas where conifers were relatively more abundant, attaining 35%, a proportion still considerably below the 50% and 95% of conifers in grant-aided woodlands and Forestry Commission plantings. Overall, sycamore, hawthorn and Scots pine each accounted for more than 10% of the trees of the Lothian region. There are, however, conspicuous differences among the different land categories (Table 3). The introduced and fecund sycamore appears, like wych elm, to thrive in urban and lowland situations. However, in upland areas, and in keeping with comparable situations elsewhere in Scotland, its numbers are greatly decreased compared with those of birch, which is the commonest type of tree, closely followed by planted Norway spruce. Unlike sycamore and birch, the relative

TABLE 3 Estimated numbers (in thousands) of the 10 commonest trees in the burghs and lowland and upland areas of the Lothian region when surveyed in 1974-75 (Edinburgh excluded) [Good *et al.*, 1978]

	Land categories							
	Burghs		Lowland rural		Upland rural		Total	
Rank in descending order of frequency	Types of tree	Estimated number of trees	Types of tree	Estimated number of trees	Types of tree	Estimated number of trees	Types of tree	Estimated number of trees
1	Sycamore	41 *(18.4%)*	Sycamore	470*(15.3%)*	Birch	330*(15.6%)*	Sycamore	630*(11.6%)*
2	Wych elm	18 *(8.4%)*	Hawthorn	410*(13.3%)*	Norway spruce	320*(15.1%)*	Hawthorn	600*(11.1%)*
3	Hawthorn	16 *(7.3%)*	Scots pine	340*(11.1%)*	Scots pine	220*(10.7%)*	Scots pine	570*(10.5%)*
4	Elder	14 *(6.5%)*	Wych elm	230 *(7.4%)*	Hawthorn	170 *(8.1%)*	Birch	430 *(8.0%)*
5	Birch	11 *(5.1%)*	Sitka spruce	210 *(6.7%)*	Ash	170 *(8.1%)*	Norway spruce	400 *(7.3%)*
6	Rowan	10 *(4.4%)*	Ash	200 *(6.4%)*	Beech	150 *(7.0%)*	Ash	380 *(7.0%)*
7	Oak	10 *(4.4%)*	Larch	200 *(6.4%)*	Sycamore	120 *(5.5%)*	Wych elm	350 *(6.5%)*
8	Flowering cherry	9 *(4.2%)*	Elder	190 *(6.1%)*	Wych elm	100 *(4.7%)*	Larch	280 *(5.2%)*
9	Ash	9 *(3.9%)*	Beech	120 *(4.0%)*	Willow	100 *(4.7%)*	Beech	270 *(5.0%)*
10	Apple	8 *(3.4%)*	Willow	120 *(3.8%)*	Larch	80 *(3.8%)*	Sitka spruce	250 *(4.6%)*
	Others	75 *(34.0%)*	Others	600*(19.3%)*	Others	350*(16.7%)*	Others	1250*(23.2%)*
	Total (thousands)	200*(100%)*	Total	3100*(100%)*	Total	2100*(100%)*	Total	5400*(100%)*

* Percentages computed for vertical, within land category, comparisons.

abundance of Scots pine in rural areas was not affected by altitude, being the third commonest tree in both situations. It was, however, conspicuous by its absence in urban localities. Oak was relatively more important in the burghs than in the rural areas, although it was nowhere plentiful.

Of the 1.4 million trees in burghs, 0.9 million occurred in Edinburgh with 71,000 in streets and public parks and 820,000 in gardens. The latter, as already mentioned, were strongly influenced by social factors. Numbers increased from 20 ha^{-1} where home ownership ranged from 0-25% to 115 ha^{-1} where most houses were owner-occupied. Street trees were relatively important where few houses were owner-occupied, forming 23% of the total, but only 1% at the other end of the scale of home ownership (Plates 6 and 7).

Possibly reflecting social attitudes, the numerically important apple (domestic and crab), lilac, flowering cherry, rowan, cupressus and laburnum of Edinburgh were replaced in more rural burghs by sycamore, wych elm, hawthorn, birch, oak and ash (Table 4).

TABLE 4 Estimated numbers (in thousands) of the 10 commonest trees in Edinburgh compared with those in other burghs of the Lothian region (1972-75) (Good *et al.*, 1978).

Edinburgh		Other burghs	
Apple, domestic	140	Sycamore	41
Lilac	81	Wych elm	19
Flowering cherry	66	Hawthorn	16
Sycamore	65	Elder	14
Rowan	56	Birch	11
Cupressus	45	Rowan	10
Apple, crab	44	Oak	10
Beech	41	Flowering cherry	9
Laburnum	40	Ash	9
Birch	37	Apple	8

NB The 10 commonest trees account for 64% of the total in Edinburgh and 66% of those in other burghs.

When diameters at breast height (dbh) were arranged in 5 classes, it was found that there were more small (0-20 cm) than large trees (> 20 cm) (Figure 8). However, these data reflect not only differences attributable to age but also innate differences associated with different species. Thus apple, blackthorn, common alder, etc....never exceeded 40 cm dbh, while maples, cotoneaster, Douglas fir, elder, etc ..., were always less than 80 cm dbh, a size sometimes exceeded by ash, cedar, horse-chestnut, etc. On closer examination of individual species, it appeared that the size class distributions of species such as sycamore and ash would ensure their conservation, but this relationship was not observed for other species, including oak and lime. This imbalance was particularly noticeable in parks, where virtually all Scots pine were larger than 20 cm dbh. In hedgerows, there was a dearth of small oaks and wych elms (even before the advent of Dutch elm disease), contrasting with less extreme size class distributions of beech and ash. Could it be that the more successful beech and ash, unlike wych elm and oak, are better able to withstand modern methods of management involving repeated machine trimming?

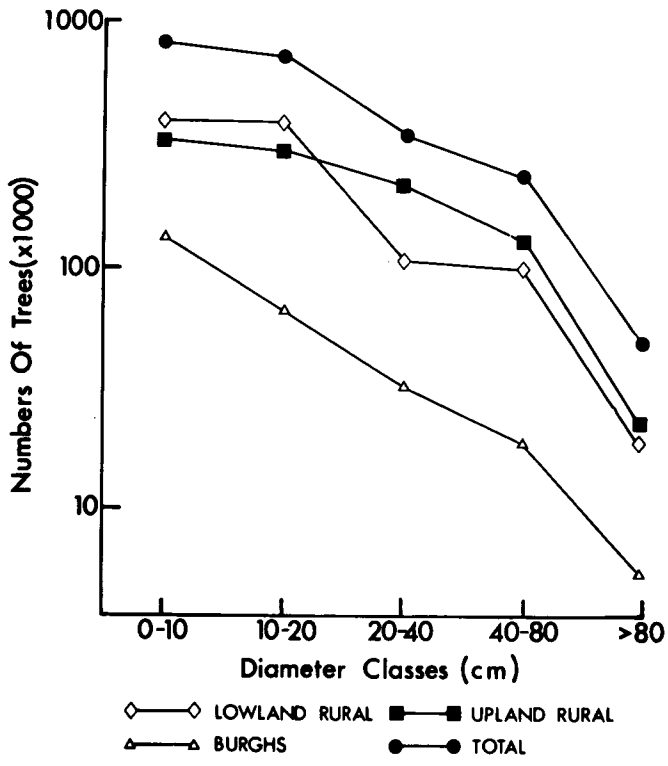

Fig. 8 *Frequencies of diameter classes among trees in different land categories of the Lothian region (Good* et al., *1978).*

Assessments of utility were confined to trees in Edinburgh greater than 30 cm in diameter (dbh), 73,000 of the total of 1 million. Of these trees, 11%, 78% and 11% were graded of good quality, utilisable and non-utilisable, respectively. As it happens, sycamore and wych elm together accounted for 66% of the trees larger than 30 cm in diameter, a proportion suggesting that the visual amenity of Edinburgh may be seriously impaired if its elms are stricken by Dutch elm disease– the really significant trees, in a landscape sense, are of too few species.

2. Implications

There is a large tree resource in the Lothian region, whether judged in terms of amenity, fuel or processable timber. Doubtless, this finding has its parallels elsewhere in Britain. The resource needs to be conserved, not preserved, and positive action should be taken to ensure conservation. However, the development of a fully integrated programme of management (to sustain) is sometimes vitiated by problems attributable to land ownership. Ways must be found of gaining the continuing support of private and public owners, and of reconciling agricultural and forestry interests with those of nature conservation, landscape, general amenity and timber and fuel production. It may be possible to conceive a management plan for trees in a city such as Edinburgh by attempting to reconcile these interests with the attention being paid to the possible use, of some, for timber or fuel. Experience of Dutch elm disease should be sufficient to stress the need for species diversity to minimize the calamitous landscape effects that occur when a tree species becomes severely depleted. At the same time, management plans should make provision to allow successional plantings, a procedure that would incidentally hasten conservation in contrast to the imposition of preservation, often by Tree Preservation Orders.

Hedgerows are an important component of lowland landscapes in the Lothian region and of much of Britain, having particular significance in intensive arable areas, where woodlands, scrub and parkland trees are few in number. It might be expected, as has often been argued, that trimming would preclude regeneration; in the event, this appears to be true for oak and wych elm, but appreciable numbers of beech and ash saplings seem to develop. The strong apical control in beech and particularly in ash leads to the rapid development of a few strong shoots which may develop into substantial saplings between cuts, whereas oak and wych elm generally respond to trimming by producing masses of competing shoots.

The parks or 'policies' (planted areas surrounding country mansions, mostly landscaped in the 18th and 19th centuries) are an important feature, albeit limited in extent, of the Lothian region. There is, however, good reason to question their management, and of those elsewhere in Britain, because their continued beauty could be in jeopardy without some semblance of successional planting. (Plate 8).

Before really effective management of amenity trees can be instituted, much more needs to be known about their biology. Whereas much is known about the growth of a limited variety of trees cultivated in plantations, we are virtually ignorant of the growth of the many species of amenity trees, each of which may be nurtured in a diverse array of sites. At present, life tables are being prepared for some species, linking life expectancy with the relation between age and size. But perhaps more important than this is the need to win the support of, and bring together, all sections of the population, often with apparently conflicting interests. With this support the problems of establishing programmes of sustained management are lessened. The aim should be a proper transfer of interest from preservation to conservation, a change which would incidentally necessitate successional thinnings, so releasing a supply of wood, a renewable, but admittedly restricted, source of timber and fuel.

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4. HEDGEROWS AS A RESOURCE

M.D. HOOPER

At the end of the 1950s, the national stock of hedges in England and Wales amounted to about 500,000 miles (804,672 km) (Locke, 1962), their character and distribution differing in different parts of the country (Pollard *et al.,* 1974). East Anglia had the fewest hedges, mainly of hawthorn *(Crataegus monogyna).* There were more hedges in the mixed farming areas of the Midlands, where, although hawthorn was still dominant, elm (*Ulmus* spp) was locally frequent. The greatest density of most diverse hedges occurred in the pastoral areas of the west, with pockets of beech *(Fagus sylvatica)* hedges in the upland areas, eg Exmoor. During the last 25 years, many miles of hedgerow have been lost (Hooper, 1970*b*; Baird & Tarrant, 1973; Davis & Dunford, 1962; Cowie, 1970; Westmacott & Worthington, 1974; Williamson, 1967). The precise rates of loss have been the subject of discussion. In the period from 1945 to 1970, the average loss in England and Wales was 5,000 miles/year (8,047 km/year), with a peak rate, measured over a few years around 1965, approaching 15,000 miles/year (24,140 km/year). Although there were local variations, the impact of these losses has been greatest in eastern England, which initially had fewest hedges. It seems that lengths of hedgerows in the arable lands of eastern England have been halved since 1945.

1. Hedgerow trees

Like hedgerows themselves, populations of hedgerow trees have detectably decreased in recent years. Westmacott and Worthington (1974) showed that only 47% of hedgerow trees present in 1947 remained in 1972. In Huntingdonshire the percentage was 20%, and, in Herefordshire, 80%. From the 1965 census of hedgerow and park timber made by the Forestry Commission, it was estimated that the timber resource amounted to 946 million hoppus feet (34 million m^3), which, at the time, exceeded the volume of Forestry Commission woodlands.

Accepting that Forestry Commission woodlands contain quantities of young developing trees, the hedgerow timber resource is nonetheless appreciable. It is unlikely, however, to sustain itself without intervention, the larger numbers of overmature trees being matched by insufficient young trees (Locke, 1970).

From Table 5 it is clear that only in 1951, after the war period when hedgerow trimming had not been carried out effectively, was there a significant proportion of saplings for recruitment to older age classes. Even the ratio of 2:1:1:1 was held by the FC to indicate that the total volume of hedgerow timber would ultimately diminish through insufficient recruitment of young trees (Forestry Commission, 1953) and the most recent survey indicates an even distribution. There is, however, considerable variation between species, as is indicated by a small survey carried out in north Northamptonshire (see Table 6).

TABLE 5 Proportions of hedgerow trees in 4 age classes in census made by the Forestry Commission.

	Age classes			
Dates of Census	Saplings	Young	Middle Aged	Mature Trees
1955	24	29	24	23
1951	42	19	19	20
1942	24	30	22	24
1918	33	21	19	27

TABLE 6 Age class distributions of 3 hedgerow tree species in north Northants in 1951.

	Age classes			
	Saplings	Young	Middle Aged	Mature Trees
Ash	25	25	29	17
Oak	15	15	25	45
Elm	0	20	10	70

The relative abundance of the species varies in different parts of the country. In the 1951 FC census, the sampling frequency was too low to show fine details of species composition and an even lower sampling frequency was used in 1965-67 (Locke, 1970), omitting many areas with relatively few trees. Details in terms of volume are available for 1951 (Table 7).

TABLE 7 Distribution (%) by volume of different hedgerow tree species in England, Scotland and Wales when counted in 1951.

	England	Wales	Scotland
Conifers	6.5	12.5	9.1
Oak	31.4	31.2	24.2
Ash	12.6	11.4	21.6
Beech	8.2	4.4	25.7
Elm	21.3	13.3	2.0
Birch	0.3	1.0	0.5
Sycamore	6.0	14.8	11.6
Chestnut	0.4	-	-
Others	13.3	11.4	5.3

2. Purposes and evaluation

Hedges and hedgerow treees have many uses—to delimit areas of land and control the movement of farm animals, to provide shelter for crops and stock, to act as a timber resource, etc. However, their value for shelter within the UK should not be taken for granted. Although there is a considerable continental literature giving many instances where shelter has increased the profits from crop plants and animals, the evidence from British conditions is less persuasive (Marshall, 1967; Shepherd, 1970). On balance, experimental evidence suggests that shelter is only justified in exceptional circumstances, such as the protection of field crops of valuable bulbs in the south west of England and when seeking early yields of strawberries and raspberries. For example, Waister (1970) found an increase in yield averaging 27% for raspberries and a mean increase of 71% in the yield of strawberries attributable to shelter. In some Narcissus cultivars, the response to shelter was insufficient to justify providing new shelter, but, in other cases, increase in dry bulb yield might justify such provision (MacKerron & Waister, 1975). In conditions similar to those in Britian, Barloy *et al.* (1977) found that shelter decreased yields of rye-grass in some years and increased them in others, but shelter consistently increased the amounts of dry matter produced by maize yet decreased grain yields. The work of Russel and Doney (1970) also calls into question the value of shelter for farm animals, suggesting that hedges have been overvalued as a source of shelter. While exposed animals require more food to maintain body temperature and live weight than do sheltered animals, the cost of the extra food in monetary terms is small compared with the costs of providing shelter. Though hedges undoubtedly affect wind profiles and soil moisture, the effects are rarely of a magnitude in Britain to alter the patterns of erosion of even the most susceptible soils, the fen peats (Sneesby, 1970).

The potential timber value of hedgerow trees has been realized for a considerable period of time (eg Merthyr Report, 1955) and emphasized, together with amenity values, in the Countryside Commission's study of New Agricultural Landscapes (Westmacott & Worthington, 1974). However, despite this recognition, it is generally believed that costs are too high to justify a systematic approach, although there are signs that changes wrought in the landscape by Dutch elm disease may lead to a greater demand for positive action.

It has been alleged that hedges are a source of pest species and provide beneficial insects such as pollinators and predators of pests. Although there is evidence to support all these roles (Lewis, 1969; Deveaux, 1977; Karg, 1977; Mesquida, 1977), each being upheld in specific instances, it is still inadvisable to make generalisations (Pollard, 1971),

3. Resource for conservation

In addition to considerations of shelter and timber, which can be evaluated fairly readily in financial terms, hedges and hedgerow trees are held in high esteem by conservationists, especially those interested in birds, many of which nest in hedgerows and are therefore vulnerable to hedgerow losses. However, it seems that bird densities, in terms of individuals or species, reach a plateau when there are about 8 or more miles (12.9 km) of hedge per square mile (Hooper, 1970*a*). It seems that competition for nesting sites is not a factor limiting birds on farmland when there are many hedges, but, below a critical hedgerow frequency, numbers of bird species and individuals fall rapidly—an indicator of competition for nesting sites. While this interpretation has been criticized (Murton & Westwood, 1974), similar observations have been made in Brittany. In areas with small fields, there were 99 pairs of 40 species on 10 ha. Where fields were of moderate sizes there were 62 pairs and 40 species, whereas, in areas with large fields and low hedgerow densities, there were only 35 pairs of 23 species on 10 ha (Constant *et al.*, 1977). Also, in Brittany, Le Duc (1977) found that populations of the tawny owl *(Strix aluco)* only decreased when fields were enlarged beyond 5.8 ha, although, in this instance, limitation of food supplies (eg the bank vole, *(Clethrionomys glareolus)*) may be of more significance than competition for nesting sites. This evidence is not to deny that Murton and Westwood (1974) made a valid point that, on a larger scale, it is the populations of birds in woodlands which are of importance to the survival of the species in the long term. This observation is supported by individual studies on populations of blackbirds (Parslow, 1969), wrens (Williamson, 1969) and titmice (Krebs, 1971), as well as by Murton's own work on the pigeon.

Much of the work with birds contains an implicit assumption that all hedges are equal, but Moore *et al.* (1967) indicated that hedges with many species of trees and shrubs also have larger populations of birds. In following this theme, it was found that numbers of tree and shrub species in a hedge increased in a predictable manner with the age of the hedge (Hooper, 1970*c*). In hedgerow samples taken over a wide area of southern England, from Devon through Gloucester to Cambridge and north to Lincolnshire, the regression formula was age = (110 x no. spp) + 30, with a correlation coefficient of 0.85, indicating that some 72% of the variation in species richness could be accounted for

by the factor of age alone (Figure 9). At least part of the remaining 28% of the variation may be caused by the wide geographic range from which the samples were taken. In a more limited area on the Huntingdon/Northamptonshire border, the correlation coefficient was +0.92 and the regression equation for predicting the age of a hedge from the number of species in a 30 yard length was age in years = (99 x no. spp) - 16. That is a 2 species hedge is 182 years old, a 4 species hedge is 380 years old and a 10 species hedge is 974 years old, but there is still variation not accounted for by the age factor, and it is improper to say that every 10 species hedge is 974 years old. We should say that 95% of 10 species hedges are between 800 and 1150 years old and that their mean age is 974 years. Clearly, a 7 species hedge could be the same age as a 10 species hedge, but it is extremely improbable that a hedge with 5 species or less in a 30 yard length is Saxon in origin. Though this relationship has been queried, the general rule of diversity increasing with age has been confirmed (Hewlett, 1973; Addington, 1978).

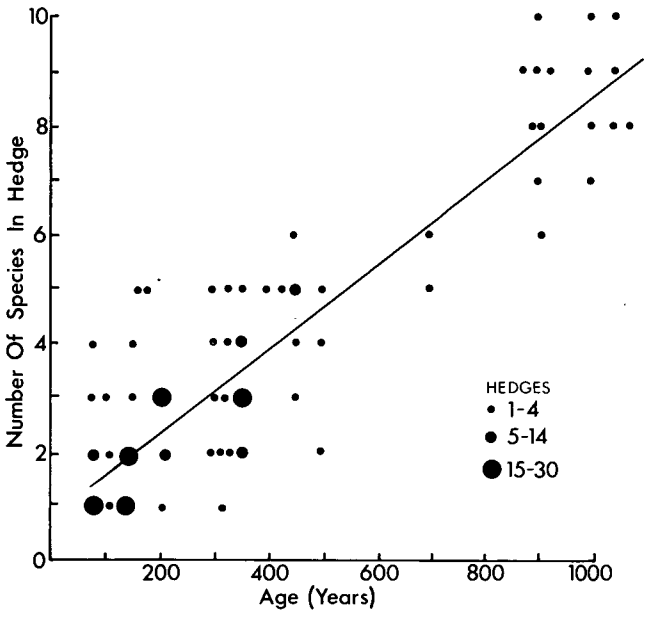

Fig. 9 *Relation between hedgerow age and numbers of different tree and shrub species in 30 yd (24.7m) lengths: the solid circles of different sizes give an indication of frequency distribution in a sample of 227 hedges assessed in Devon, Lincolnshire, Cambridgeshire and Northamptonshire (from Pollard* et al., *1974).*
Reproduced by kind permission of the publishers of "Hedges" (New Naturalist Series) by Pollard E., Hooper M.D. and Moore N.W. 1974. London, Collins.

The association with herbaceous plants is less well known, but Pollard (1973) discovered that the presence of the woodland dog's mercury *(Mercurialis perennis)* and bluebell *(Endymion non-scriptus)* in hedges is limited to hedges which are, or were, associated with woodlands. From these examples, it is clear that much can be learnt about former land use from studies of the species within hedgerows—they are a source of useful information to the historical ecologist.

The benefits and alleged benefits of hedges and hedgerow trees have at some stage to be set against their costs. In England and Wales the total annual costs of hedgerows, taking into account the land they occupy which is therefore lost to commercial cropping, together with the maintenance costs, must be *c* £25 million. Is this acceptable?

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Forest and woodland dynamics

5. WOODLAND REGENERATION WITH EXAMPLES DRAWN FROM INVESTIGATIONS OF OAK WOODLAND

M.W. SHAW

The meaning of the term "regeneration", as applied to woodlands, extends beyond mere reproduction to include germination of propagules and subsequent growth and survival of young trees until they are reasonably established (ie the immediate probability of mortality is low). This usage is in accord with the dictionary definition 'to bring into renewed existence'. Also, because the term is rarely applied to individuals but rather to populations of trees (ie woodlands), the study of regeneration may be regarded as an exercise in population dynamics. Old trees die, or are harvested, and are then replaced by young trees by:

true natural regeneration—regeneration that occurs without the intervention of man,

'foresters' natural regeneration—regeneration contrived by the use of different silvicultural practices, eg the uniform shelterwood system, the group selection system

artificial regeneration—regeneration by planting young trees grown in nurseries.

These different types of regeneration have many features in common, eg with all of them it is usually necessary to control grazing by domestic or wild animals for at least a short period. Even true natural regeneration may require control of herbivores as large predators have often been eliminated or their numbers greatly depleted.

To maintain the species, a tree, like other plants and animals, must ensure the survival of at least one offspring in its lifetime (on average). Thus the emphasis shifts from the high rate of success sought in agriculture, eg crops such as wheat and potatoes, to the ultimate survival of a very few individuals. In true, as opposed to 'foresters', natural regeneration, the time-scale and a surplus of replacements for silvicultural requirements, eg to encourage straight, clean (branch-free) stems and provide an intermediate harvest, are largely irrelevant. Nonetheless, reproduction is an extremely critical stage in the life process and the penalty of failure is to be replaced by another species of tree or vegetation with some other life-form. In rare cases, where reproduction fails to keep pace with mortality, extinction of species occurs. However, trees are an extreme example of reproductive longevity. Individual trees of a species such as oak may live for up to 400 years and are capable of reproducing for all but the first 25-30 years. This reproductive strategy has obvious advantages; the repeated production of seed maximising the chance of coincidence with favourable conditions for establishment (cf some bamboo species which exhibit synchronous flowering over a large area followed by death).

The difficulties of investigating the population dynamics of woodlands are considerable, the main problem being that of time-scale. Ecological changes in woodland take place very slowly and without careful, systematic recording it is difficult to determine what is happening—if anything. Sometimes it is easier to observe change in retrospect. For example, an area of woodland in north Wales gave the appearance of being even-aged. However, a study of ring growth showed that there was an age range from 100-150 years and that natural regeneration, at quite a modest density, had produced this area of woodland but had taken at least 50 years to do so. Even though this was a fairly dramatic example of non-woodland being replaced by woodland (historical evidence and early growth rates indicate this transformation), it is doubtful whether what was happening would have been obvious to the casual observer at the time.

Clearly straightforward observational or experimental investigation of woodland dynamics is out of the question because of the time-scale involved. To obtain an understanding in a reasonable period of time it is necessary to piece together evidence from the different processes involved and it is therefore essential to identify the more critical processes. For sessile oak *(Quercus petraea)* in north Wales, the most critical part of the cycle is seedling growth and survival and, in this instance, grazing by sheep is the single most important factor influencing these processes. Most woodlands in north Wales are unfenced (or ineffectively fenced) and are subject to severe grazing and browsing pressures for at least 6 months (December-June) of the year. Unless they are protected by other species less favoured for food e.g. hawthorn *(Crataegus monogyna)* or perhaps birch (*Betula* spp), or are inaccessible to sheep, eg on cliffs,

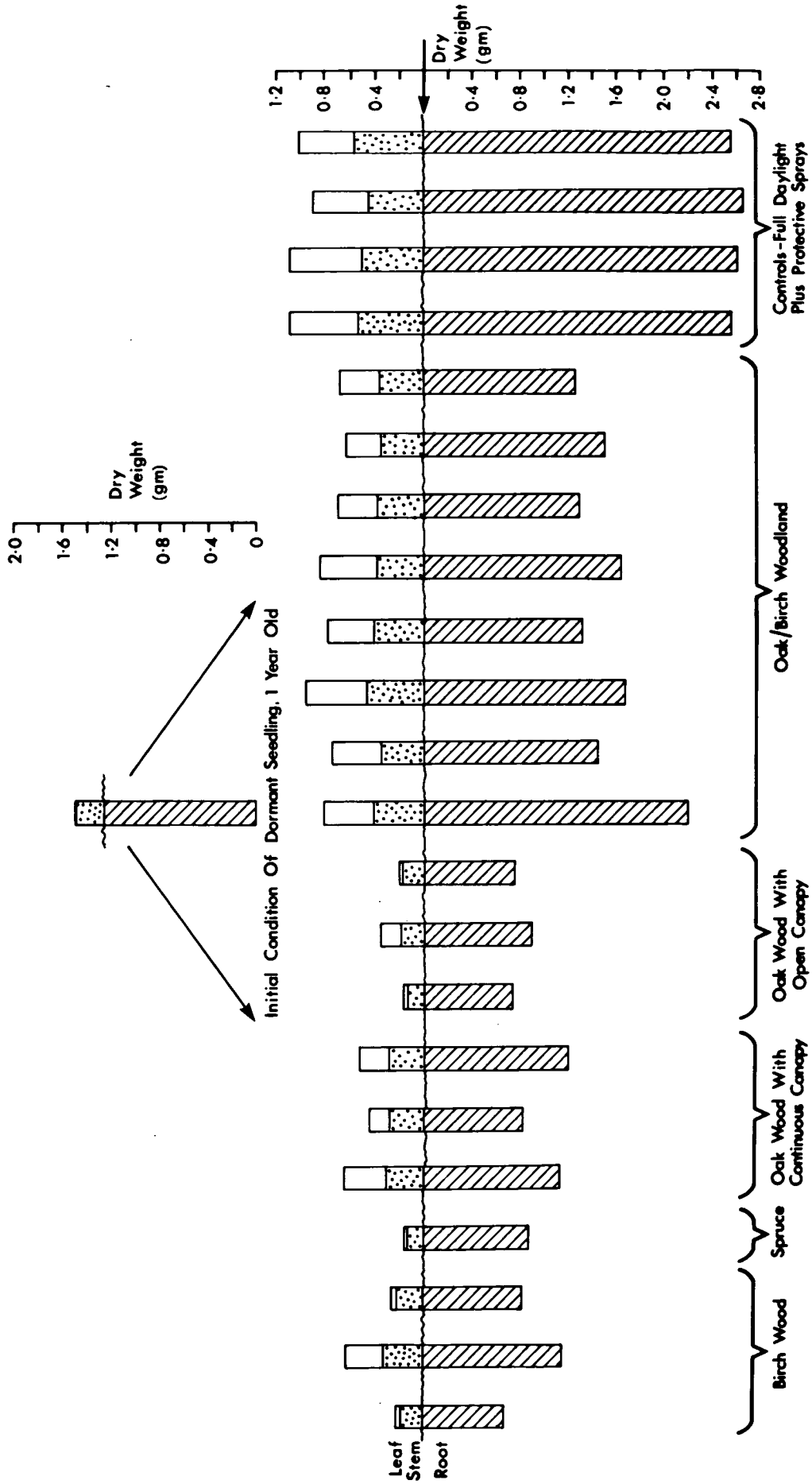

Fig. 10 *The effect on dry weight accumulation of exposing oak seedlings during their second year to different woodland conditions. For details of canopy conditions see Table 8: Saplings harvested in October.*

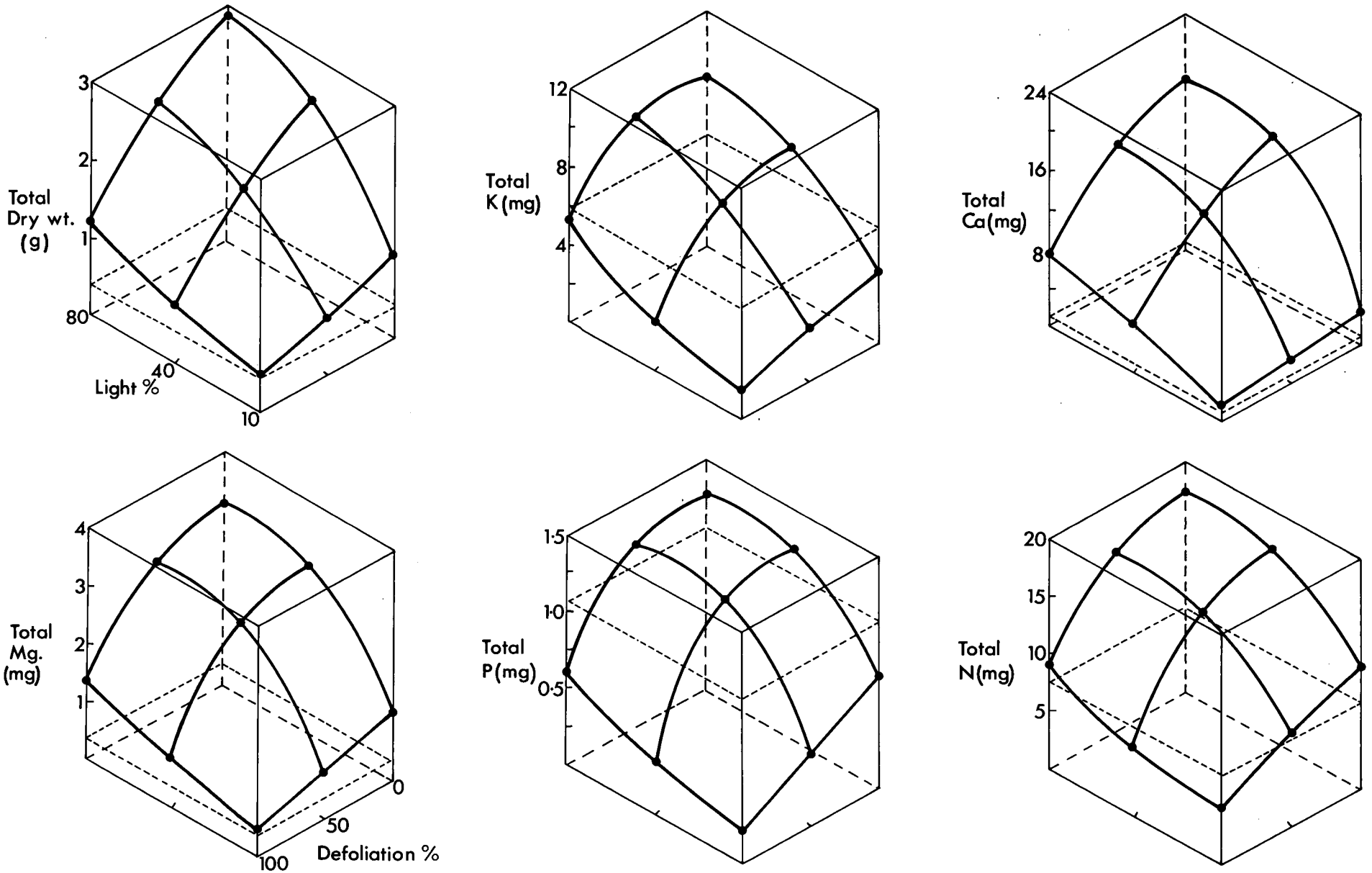

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Fig. 11 *Two year cumulative effects of defoliation and different light intensities on total dry weights of oak seedlings and their accumulations of potassium, calcium, magnesium, phosphorus and nitrogen. / Reproduced by kind permission of the publishers of "The British Oak" edited by Morris, M.G. and Perring, F.H. 1974. Faringdon, Classey.*

most young oak trees, up to *c* 5ft (150 cm) are heavily browsed. Only a minority, growing in large clearings with virtually full daylight, seem able to withstand this pressure.

1. Experimental

In the absence of grazing, or where numbers of animals are carefully controlled, the effects of tree canopy become increasingly important. The amount of light penetrating to the forest floor has an obvious influence on seedling growth and it is not difficult to determine the direct effect of this factor (see Jarvis, 1964; Ovington & MacRae, 1960). However, the presence of a tree canopy brings other problems to tree seedlings in the form of defoliating caterpillars, other invertebrates and fungi. Some of the effects of defoliating caterpillars can be measured by subjecting test oak seedlings (in pots) to various situations in a woodland. Table 8 shows the effect on leaf area and numbers of leaves/plant of a range of woodland conditions when compared with controls. The effect on leaf area is even more drastic than is indicated by the full daylight controls because oak seedlings in shade normally produce a larger leaf area in response to shade (an additional 10% under 50% daylight and 25% under 10% daylight). The cumulative effect on dry weight production of the different conditions to which the same seedlings were subjected is shown in Figure 10. There is a good deal of variability in these results, some of which defies simple explanation. Indeed, much of the variation is due to such chance events as whether a canopy tree in the immediate vicinity carried a large or small population of caterpillars in the year in question.

In more carefully controlled experimental conditions, pot-grown oak seedlings were subject to 3 different intensities of light (90%, 45% and 10% of full daylight) and 3 amounts of defoliation (0%, 50% and 100%, inflicted by cutting leaves) (see also Shaw, 1974). Effects of these treatments on dry weight accumulation and the reserves (amount/seedling) of different nutrients are shown in Figure 11. In terms of compensation point, as compared with what was contained in the original acorn, phosphorus uptake is clearly the most important factor. Potassium and nitrogen uptake can also be regarded as rather marginal for satisfactory growth. These experimental seedlings were protected against other "adverse influences", such as oak mildew and aphids, which are likely to affect most seedlings in woodland conditions. Because of this protection, the results probably overestimate seedling performance in the field but again the effect of root restriction in a pot and the absence of competing vegetation are unknown.

2. Discussion

As the above results demonstrate, the reduction of leaf area in oak seedlings has a large effect on their performance. This effect has 3 main sources (a) direct loss of material to the caterpillars, (b) impaired ability to photosynthesise during June and July and (c) the need to produce new leaves

TABLE 8 Effects of different environments on the leaf development (number and total leaf area) of pot-grown oak seedlings. Assessments made on 3 occasions. Ranges of replicates given in brackets.

		Nos. of replicates	Leaf areas (cm^2)			Leaf numbers		
			2 JULY	12 SEPT.	20 OCT.	2 JULY	12 SEPT.	20 OCT.
I	Growing in full daylight and protected with fungicidal and insecticidal sprays	4	63 *(55-67)*	78 *(65-89)*	74 *(64-84)*	8.7 *(7.5-9.7)*	12.6 *(10.3-14.8)*	12.3 *(10.2-14.2)*
II	Growing in birch wood	3	20 *(11-27)*	38 *(22-63)*	32 *(16-58)*	5 *(4.9-5.6)*	8 *(5.4-11.4)*	7 *(4.9-10.6)*
III	Growing in stand of spruce	1	2 *(–)*	5 *(–)*	5 *(–)*	2.1 *(–)*	4.8 *(–)*	1.6 *(–)*
IV	Growing in oak wood with continuous canopy	3	16 *(5-25)*	70 *(43-73)*	59 *(41-76)*	5.6 *(2.5-7.5)*	10.8 *(8.9-12.4)*	9.4 *(7.7-11.0)*
V	Growing in oak wood with open canopy	3	8 *(3-13)*	10 *(5-16)*	8 *(5-15)*	3.7 *(2.6-4.4)*	3.0 *(2.4-3.5)*	2.6 *(2.0-3.2)*
VI	Growing in oak/birch woodland	8	32 *(20-44)*	67 *(46-95)*	61 *(48-93)*	8.5 *(6.8-9.9)*	14.3 *(9.6-16.0)*	12.1 *(9.4-15.5)*

(which they do quite successfully), the use of which is restricted to about half the growing season before they are shed in the autumn. Interestingly, removal of the whole shoot system of an oak seedling at ground level in the dormant season (simulated winter browsing) has rather less effect on dry weight accumulation than 100% defoliation in May or June. The "browsed" seedling merely flushes a bud at ground level and produces a shoot system with no delay in the spring. The leaves on this shoot can then be used for the full growing season and more than compensate for the larger loss of dry matter compared with defoliation. The high root/shoot ratio typical of oak seedlings (up to 10/1 in full daylight), in which the main weight is contained in a swollen tap root, is seen as an adaptation to resist the effects of browsing.

Less is known about other factors affecting the growth of oak seedlings, in particular the effects of different amounts of soil nutrients and competition with the ground layer vegetation. Preliminary experiments with fertilizers suggest that they may only serve to intensify competition with ground-layer species (*Deschampsia flexuosa* in particular in north Wales). A reduction in root competition produced by excising all roots entering an area produces quite a marked increase in the growth of oak seedlings within this area. The main effect would seem to be through the cutting of tree roots. The effects of mycorrhizas on oaks are unknown but are suspected to be important.

Clearly some further information is required before a satisfactory model of oak regeneration could be constructed and it is a still bigger jump to understanding woodland regeneration in which a number of species are competing. It may also be important to understand the performance of individual seedlings rather than work in terms of the mean seedling. Oak seedlings seem to be particularly variable in their growth strategy eg date of flushing, length of shoot produced and whether they indulge in lammas growth or not. For example, pot-grown seedlings, 2 years old can have root/shoot ratios that vary from as little as 2/1 to 10/1 and flushing dates can vary by as much as 6 weeks from first to last. In the field, seedlings behave with similar variability and this variation may explain why the occasional seedling survives and continues to make slow growth long after others have died. Extreme physiological variation and selection may be an important factor in the success of oak as a widespread tree in British woodlands.

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6. CHANGES IN THE GROWTH AND STRUCTURE OF A YOUNG PLANTATION FOREST

E.D. FORD

Whilst it may seem obvious that weather has a strong influence on tree growth—indeed the whole science of dendrochronology is based on this assumption—it has sometimes been observed that trees of the same species in a region may not respond in the same way to variations in weather. This difference in response can be due to differences in physiology between young and old individuals, but the microclimates in which individuals are found are perhaps the major factors. As a forest grows its microclimate changes, for example the amount of foliage increases, so that a larger proportion of rainfall is intercepted and evaporates directly back to the atmosphere without ever reaching the soil.

The structure of a forest determines its microclimate, which, in turn, regulates the amount of growth which is made by trees. Changes in both the growth rate and the structure of a young plantation of Sitka spruce *(Picea sitchensis)* were studied by measuring numbers, lengths and positions of all branches which had been formed on trees 12 years old.

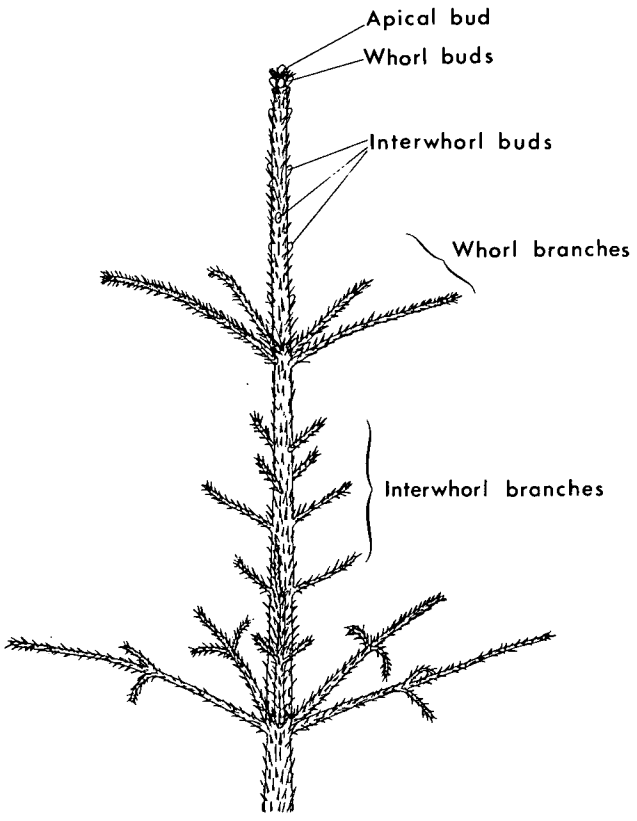

Fig. 12 *The branching structure of the terminal section of* Picea sitchensis.

Each Sitka spruce bud elongates in the spring to form a shoot on which a further set of buds develops to elongate in the following year. There are 3 types of bud: the apical bud which continues growth along the main axis of the shoot, whorl buds occurring in a cluster round the shoot below the apex, and interwhorl buds distributed singly or in small clusters along the length of the shoot. These arrays of buds are found on the main leader of each tree and vigorously growing side branches—particularly those near the top of the canopy. For branches growing further down the tree, there is a tendency first to produce fewer or no interwhorl buds, then not to produce whorl buds, until, finally, the apical bud does not form and the branch dies (Figure 12).

A scaffold was erected in a 12 year old commercial plantation of Sitka spruce, in Greskine Forest near Moffat, Scotland. A single set of measurements was made of (i) the length, (ii) angle from the horizontal and (iii) direction (compass bearing) on (a) every branch on the main stem of each of 10 trees and (b) each shoot on whorl—and interwhorl—branches representative of those at different levels within the plantation (Cochrane & Ford, 1978). Because few branches had been lost from the canopy of age 12, it was possible to obtain a comprehensive historical record of branch growth. Measurements of shoot growth and branch numbers produced from the main stem were continued for 5 years.

The annual height increment of the main shoot (the leader or leading shoot) increased gradually between years 1 and 6, rapidly between years 7 and 10, and fluctuated about an annual mean of 0.8 m in years 11-16 (Figure 13). The number of whorl buds produced at the top of the tree decreased after year 6 from around 12 to 6, and continued at that level with only minor annual variations. Two aspects of branch dispersion were assessed—(i) display in relation to the points of the compass, and (ii) angular divergence from the horizontal. Branches were distributed evenly around the main stem irrespective of the number produced. At the tops of trees, whorl branches were produced at an angle 30° above horizontal, whereas interwhorl branches were produced at only 5° above the horizontal. However, with subsequent growth and as branches became heavier and tree trunks thickened, the angles of both whorl and interwhorl branches decreased, ultimately dropping below the horizontal.

Patterns of branch extension were particularly complex. Until year 10, the growth of whorl branches seemed directly related to numbers of whorl branches which had formed. The more whorl branches the less the mean branch growth and also the less the amount of leader growth; an

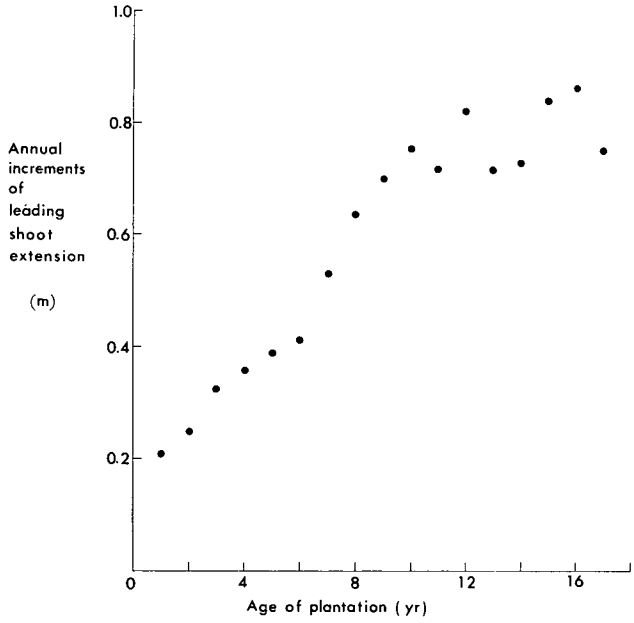

Fig. 13 *Annual growth increments of leading shoots in an ageing plantation of* Picea sitchensis.

indication that growth was determined by within-tree competition for limiting resources. After year 10, whorl branch extension from the main stem was positively related to tree height and leader extension. At this stage, growth of branches seemed to be limited by competition between trees. Interwhorl branches always extended substantially less than whorl branches; their growth was not affected by the different phases of within-tree and between-tree competition.

The critical changes in leader growth and branch production and extension, at 6/7 yr and 10/11 yr, correspond with "canopy overlap" when branches of neighbouring trees touch for the first time and "crown interlock" when branches begin to die (Figure 14). Although detailed analyses of environmental variations at these two break-points have not been made, it is suggested that, from year 7 onwards, with the establishment of a complete canopy cover, there was a marked decrease in amounts of rain reaching what was initially a very wet soil. This decrease could have increased mean soil temperatures and accelerated the mineralisation of the 'grass' cover sward, inverted during site preparation, so stimulating tree growth.

The onset of between-tree competition, as suggested by the stabilisation of mean height increment and the altered relation of branch numbers with branch extension, 10/11 yr after planting, is of particular significance as, after this time, large trees have larger relative growth rates than smaller trees. The death of branches and the maintenance of a constant amount of needles for the crop as a whole suggests that there was competition for light. This suggestion is supported by the restricted growth rates of lower branches and the development of asymetric crowns where trees were touching (Ford & Deans, 1978). In addition to competition for light, there is also evidence to suggest that the potential transpiration demand of trees 10/11 years old is in balance with the amount of water received at the soil surface during the summer months (Milne, 1979). Amounts of

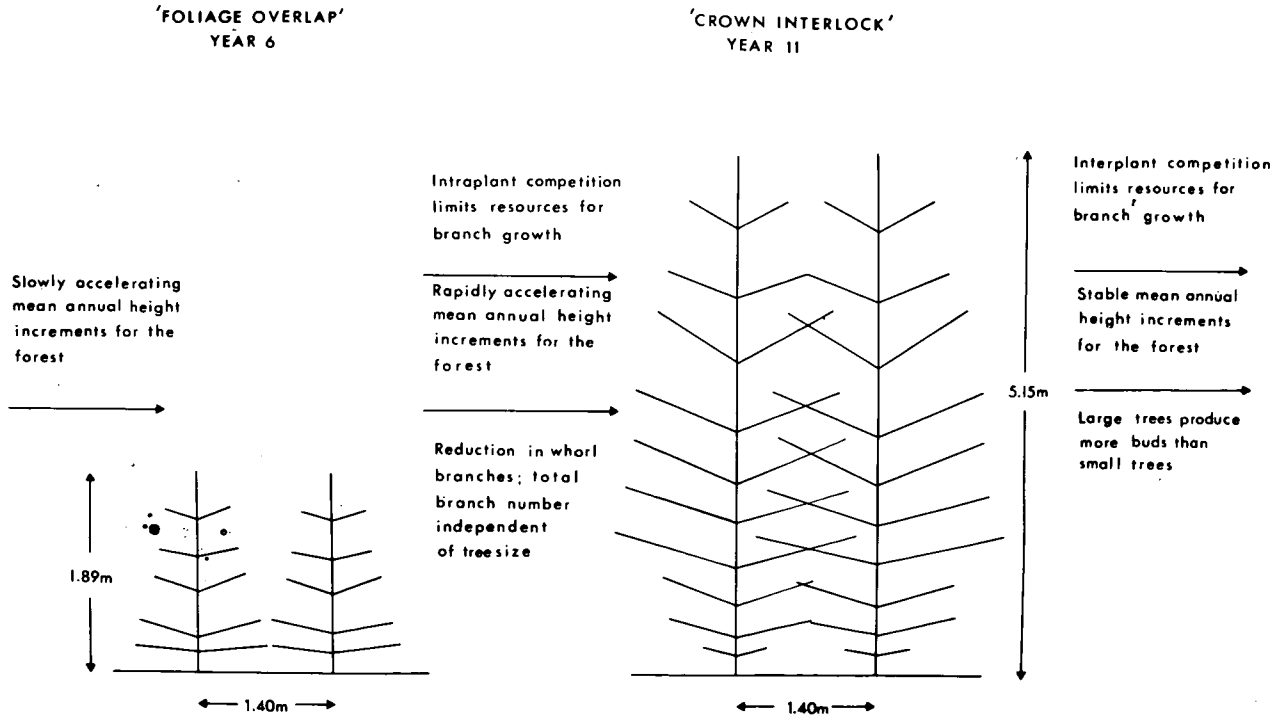

Fig. 14 *The characteristics of branch production and extension described in relation to 2 critical stages in the development of the canopy structure of a young plantation of* Picea sitchensis.

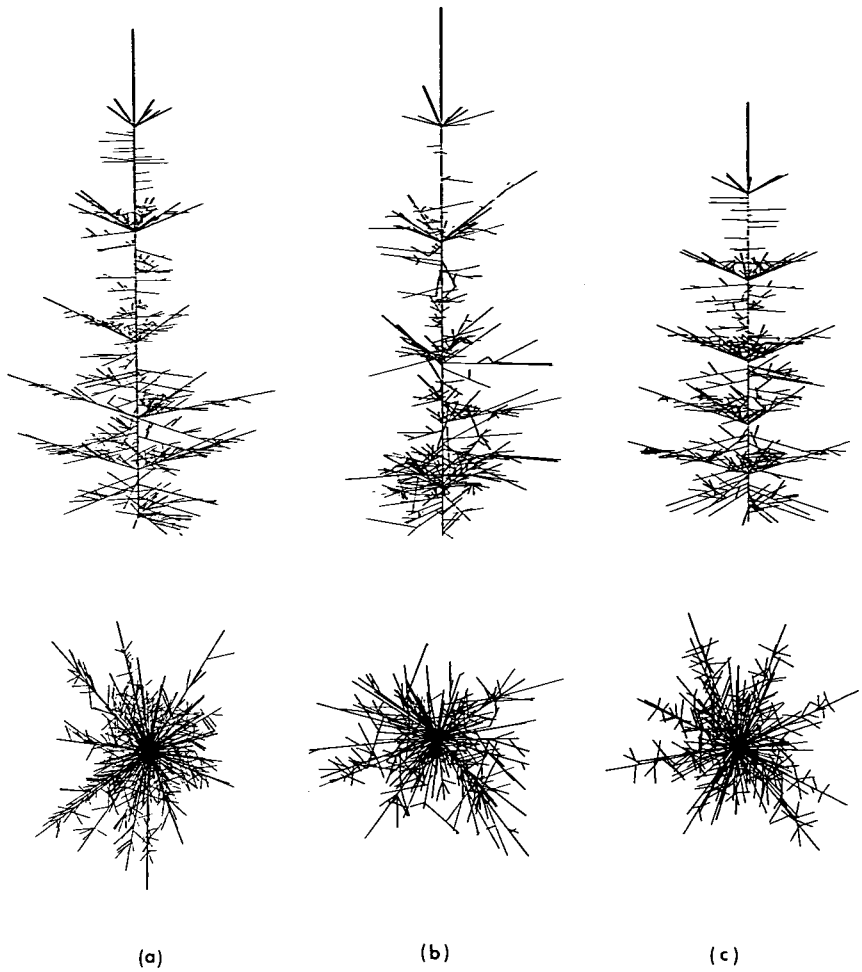

Fig. 15 *Tree structure, in elevation, and plan projections, produced from a model of branch growth with: (a) the variance of the branching rules, as calculated for a Sitka spruce plantation, (b) the variance doubled, (c) variance reduced to zero.*

stemflow in the Greskine plantation are relatively large, possibly because the upper branches are conspicuously upright. They are positively correlated with crown size (Ford & Deans, 1978) and contribute a major part of the water used in the transpiration stream. Large trees may not only intercept more radiation but may also have access to more of the water available for uptake.

The inter-relationships between bud production, dispersion and elongation were studied with sufficient accuracy for them to be expressed in a series of mathematical relationships—each with a calculated variance. These relationships have been used in a computer model so that the growth of a young tree can be simulated. In the first instance, this model has been used to examine just how regular is tree form. If, on the other hand, the variance associated with each relationship is reduced to zero, the tree appears less like a Sitka spruce and, in some respects, more like a fir. If the variance is increased to greater than that measured, then the tree loses its form (Figure 15). Further uses for this model might include the assessment of the effect of reducing whorl branch number, which is at least partially under genetic control, and the effect of this reduction on total branch length. If numbers of whorl branches were decreased, then numbers of knots appearing in the timber would also be decreased. This would be a valuable achievement, but the reduction in the number of branches would also decrease the photosynthesizing area of the tree and limit potential growth.

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7. MONITORING IN WOODLANDS

J.M. SYKES

The aims of monitoring include the detection, measurement and assessment of changes which may be occurring in the abiotic (physical and chemical) and biotic components of ecosystems. In practice, because of limited resources, human, financial, or both, the monitoring of woodlands will usually be confined to a small number of soil characteristics, possibly a few faunal samples and principally to floral studies often limited to vascular plants but sometimes including bryophytes and lichens. Answers are sought to a number of questions which basically are the same for all types of ecological surveys:

a. What is there?

b. How many of them are there?

c. How big are they?

d. Where precisely are they?

Whether or not change will be detected, depends on the precision with which attributes and variables are measured and their rates of change in relation to the time span between measurements. Clearly it will be impossible, because of the size of most woodlands, and in most instances unnecessary, to answer these questions for the entire ecosystem and therefore a system of sampling is used. Nonetheless, in some intensively-managed woodlands it is desirable and feasible to make a total enumeration of trees.

In common with other types of survey, monitoring requires that samples should be representative, and, additionally, relocatable so as to minimize the confounding effects of spatial and temporal variations. These considerations have led to the use of systematically arranged samples, a procedure giving good overall coverage, enabling relocation and providing a suitable framework for the selection of additional samples if required. At present a number of woodland sites are being monitored among which are Kirkconnell Flow NNR, Kirkcudbrightshire, and Stone Chest, Cumbria. At the former, baseline survey data have been collected in a systematic fashion and provide reasonably detailed information on within-site variation at a single time; at Stone Chest, Cumbria, the element of temporal variation has been added by making repeated surveys.

1. Kirkconnell Flow NNR, Kirkcudbrightshire

This site occupies a rectangular area of 155 ha. It is a partly-wooded, estuarine raised bog, lying 9 m above sea level, with 100 cm annual rainfall. The survey attempted to describe and map existing vegetation and record changes in mire vegetation and stands of pine and birch. A systematic grid with intersections at 100 m was used to locate samples. Nested quadrats from 4 m^2 to 200 m^2 were placed at each intersection for the listing of species and estimation of their cover or site occupancy. In total, there are 159 sample locations which were examined by a 2-man team completing 12 samples per day. When classified, the floral data resulted in 8 recognizable groups of quadrats identified by indicator species which are not necessarily dominants. Lists of species which are constant in each of the 8 groups are shown in Table 9 where it can be seen that *Calluna vulgaris* is the only ubiquitous species. Other plants tend to be characteristic of Groups 1-4 or of Groups 5-8. These 2 major groupings represent, on the one hand, the vegetation of the central wet bog or that associated with peat cutting activities immediately surrounding the central area, and, on the other hand, that of the peripheral and drier area, parts of which have a developing woodland flora. Using these groups, it was possible first to estimate the proportion of the NNR occupied by each of the 8 vegetation groups by equating it with the proportion of sample plots falling into each of the groups, and second to produce an estimated reconstruction of the pattern of vegetation as reflected in the spatial distribution of the vegetation groups. This reconstruction can be achieved by (i) the interpolation of freehand lines to approximate boundaries or (ii) the use of an explicit rule, often a nearest-point rule, requiring that a point should be assigned to the same group as its nearest-neighbour sample point.

Where an area is divided into a number of squares and the vegetation sampled at the centre of each square, it may be assumed that the vegetation at the centre is typical of its entire square (Figure 16). Intuitively it would be expected that the real pattern of vegetation would be more faithfully reconstructed if the sample points were closer together and the squares therefore smaller, particularly if the mosaic were on a small scale. Using the vegetation classification it was possible to construct a dichotomous key based on the presence of numbers of contrasting species at each dichotomy (Table 10). Next, by visiting a new series of sample locations at the centre of a square formed by each 4 of the previous samples, the number of samples was doubled. On this occasion, however, there was no need to compile lists of species; instead the vegetation was classified by the presence or absence of indicator species in the dichotomous key. In this way it was possible to complete approximately 40 samples per day, as compared with the original 12, with the cost effective production of a map giving the spatial distribution of the 8 vegetation groups (Figure 17).

TABLE 9 Constant species in 8 vegetation groups at Kirkconnell Flow NNR

Species	Group 1	2	3	4	5	6	7	8
Calluna vulgaris	✓	✓	✓	✓	✓	✓	✓	✓
Erica tetralix	✓	✓	–	✓	✓	–	–	–
Eriophorum angustifolium	✓	✓	✓	✓	–	–	–	–
Eriophorum vaginatum	✓	✓	–	✓	–	–	–	–
Oxycoccus palustris	–	✓	–	–	–	–	–	–
Pinus sylvestris	✓	✓	–	✓	✓	–	–	–
Andromeda polifolia	✓	✓	–	–	–	–	–	–
Odontoschisma sphagni	✓	–	–	✓	–	–	–	–
Pleurozium schreberi	✓	✓	✓	✓	✓	–	–	–
Sphagnum palustre	–	✓	–	–	–	–	–	–
Dryopteris dilatata	–	–	–	–	✓	✓	✓	–
Galium saxatile	–	–	–	–	–	–	–	✓
Holcus lanatus	–	–	–	–	–	–	–	✓
Molinia caerulea	–	–	–	–	–	✓	–	✓
Oxalis acetosella	–	–	–	–	–	–	✓	–
Rumex acetosella	–	–	–	–	–	–	–	✓
Sorbus aucuparia	–	–	–	–	–	–	✓	–
Betula pubescens	–	✓	✓	✓	✓	✓	✓	✓
Leucobryum glaucum	–	–	–	–	✓	–	–	–
Dicranum scoparium	–	–	✓	✓	–	✓	–	–
Polytrichum formosum	–	–	–	–	–	✓	–	–
Vaccinium myrtillus	–	✓	–	–	✓	✓	–	–

By doubling the numbers of samples, some areas which appeared previously to be homogeneous were found not to be; this change of status could be important if some, but not all, vegetation groups were to be managed in a particular way (Table 11). Because the stands of pine and birch and their development in time are of particular interest at Kirkconnell Flow, it was necessary to collect additional information on the structure of these stands in different regions of the site, the locations to be sampled being selected using the 8 vegetation groups as strata. The diameter, height, and crown size, and position of individual trees were recorded, as were the numbers of saplings and seedlings (Figure 18).

TABLE 11 Area estimates, as percentages of the total area, of the 8 vegetation groups at Kirkconnell Flow using different grid size/sample size

No. of plots		159	312
Distance between plots (m)		100	70.7
Sampling fraction		0.2	0.4
Vegetation groups	1	17.6	19.2
	2	13.8	13.5
	3	12.6	13.8
	4	11.9	12.2
	5	9.4	7.7
	6	10.7	13.1
	7	15.7	12.8
	8	8.2	7.7

The distinctions between the vegetation groups are clearly seen: first, at a coarse level, the contrast between the relative importance of Scots pine and birch in Groups 6-8 both in numbers and in basal area, and secondly, at a finer level, between the numbers of Scots pine trees, saplings and seedlings in Groups 1 and 2. The vegetation in Group 2 is taken to be a successional development of that in Group 1.

2. Stone Chest, Cumbria

In the north of Cumbria the use of the Stone Chest site of 200 ha changed in 1971/72, with its ownership, from poor sheep grazing to plantation forestry. The site is unusual in some respects: although managed as a commercial enterprise by Economic Forestry (Scotland) Ltd, some concessions to normal planting practice have been made in order, it is hoped, to increase the sporting interest of the property. Thus, although 70% of the area has been planted with Sitka spruce, there are lesser plantings of other species with numbers of indigenous and exotic shrubs planted alongside extra-wide rides and metalled roads. Additionally a series of small ponds has been

TABLE 10 Dichotomous key to 8 vegetation groups at Kirkconnell Flow, based on indicator species analysis*

TYPES OF INDICATOR SPECIES

	POSITIVE	NEGATIVE
1.	Seedlings of *Sorbus aucuparia* *Dryopteris dilatata*	*Eriophorum angustifolium* *Eriophorum vaginatum* *Andromeda polifolia*

If aggregate score is: -1 or less --- (2)
0 or more --- (5)

2.	*Molinia caerulea* Saplings of *Betula* spp	*Oxycoccus palustris* *Andromeda polifolia* *Sphagnum magellanicum*

If aggregate score is: -1 or less --- (3)
0 or more --- (4)

3.	*Oxycoccus palustris* *Vaccinium myrtillus* Seedlings of *Betula* spp	*Drosera rotundifolia* *Trichophorum cespitosum*

If aggregate score is: 1 or less, assemblage belongs to GROUP 1
2 or more, assemblage belongs to GROUP 2

4.	*Eriophorum vaginatum* *Odontoschisma sphagni* *Sphagnum palustre* *Sphagnum plumulosum* *Aulacomnium palustre*	

If aggregate score is 0 or less, assemblage belongs to GROUP 3
1 or more, assemblage belongs to GROUP 4

5.	*Corydalis claviculata* *Holcus lanatus* *Pteridium aquilinum*	*Calluna vulgaris* *Erica tetralix*

If aggregate score is: 0 or less --- (6)
1 or more --- (7)

6.	Trees of *Betula* spp Seedlings of *Pinus sylvestris* *Polytrichum formosum*	Trees of *Pinus sylvestris* *Stellaria media*

If aggregate score is: 0 or less, assemblage belongs to GROUP 5
1 or more, assemblage belongs to GROUP 6

7.	*Molinia caerulea* *Potentilla erecta* *Rumex acetosella*	*Oxalis acetosella* *Vaccinium myrtillus*

If aggregate score is: 0 or less, assemblage belongs to GROUP 7
1 or more, assemblage belongs to GROUP 8

* Each indicator species present in the sample has either a unit positive or unit negative score. The aggregate score for the sample is calculated and progress through the key depends upon its value.

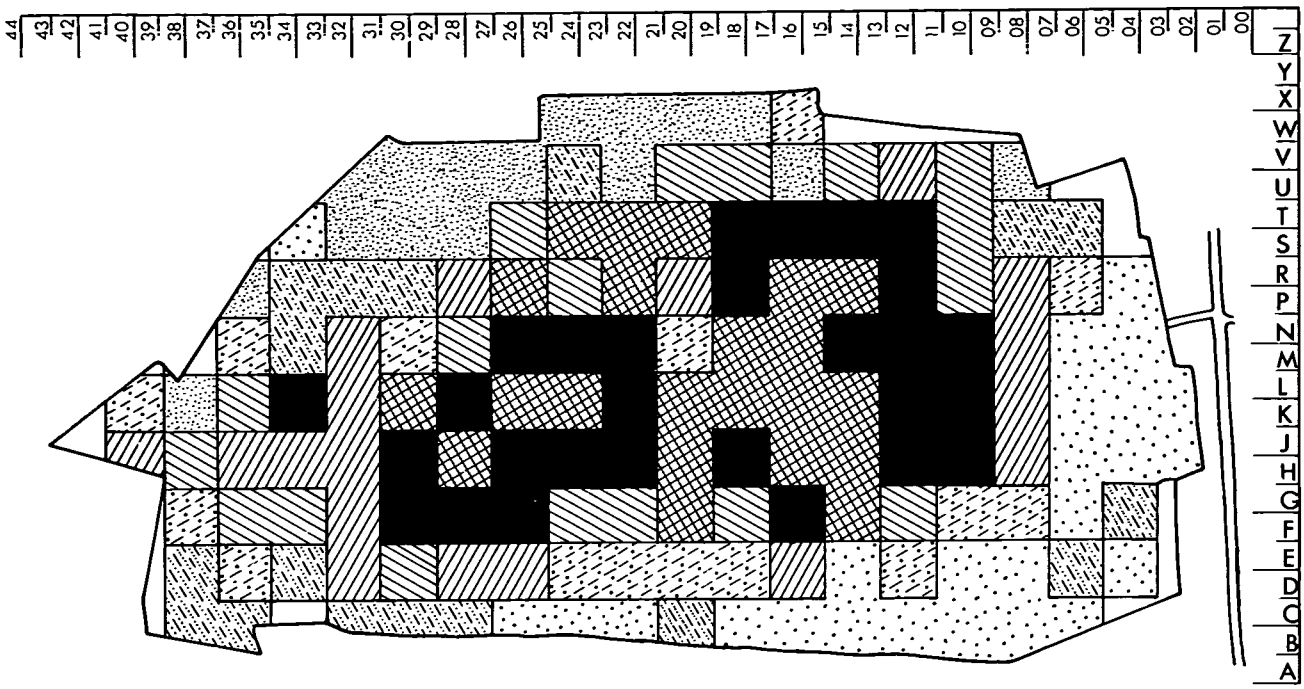

Fig. 16 *Map showing the distribution of 8 vegetation groups at Kirkconnell Flow NNR, based on samples taken 100 m apart (compare with Figure 17 where samples were taken 71 m apart). See Table 9 for Group component species.*

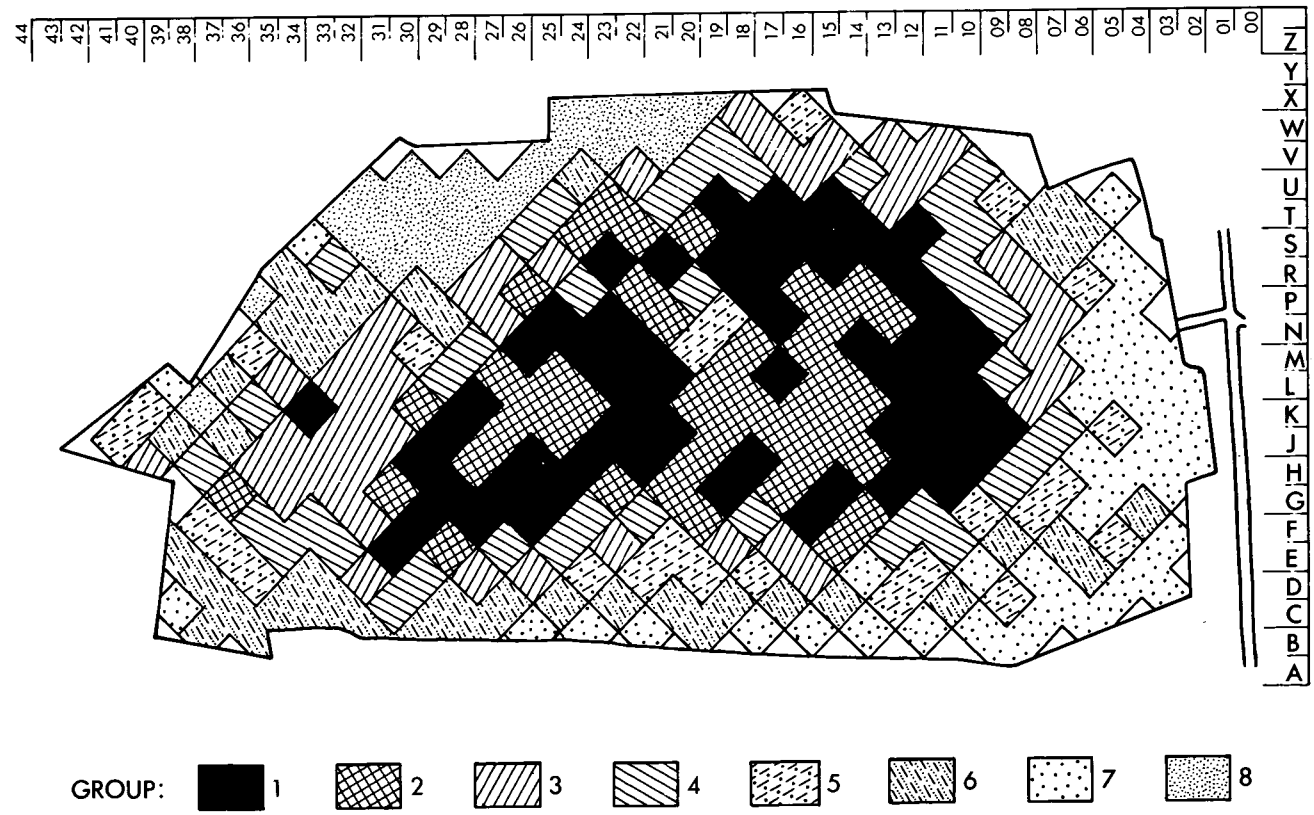

Fig. 17 *Map showing the distribution of 8 vegetation groups at Kirkconnell Flow NNR, based on samples taken 71 m apart (compare with Figure 16 where samples were taken 100 m apart). See Table 9 for Group component species.*

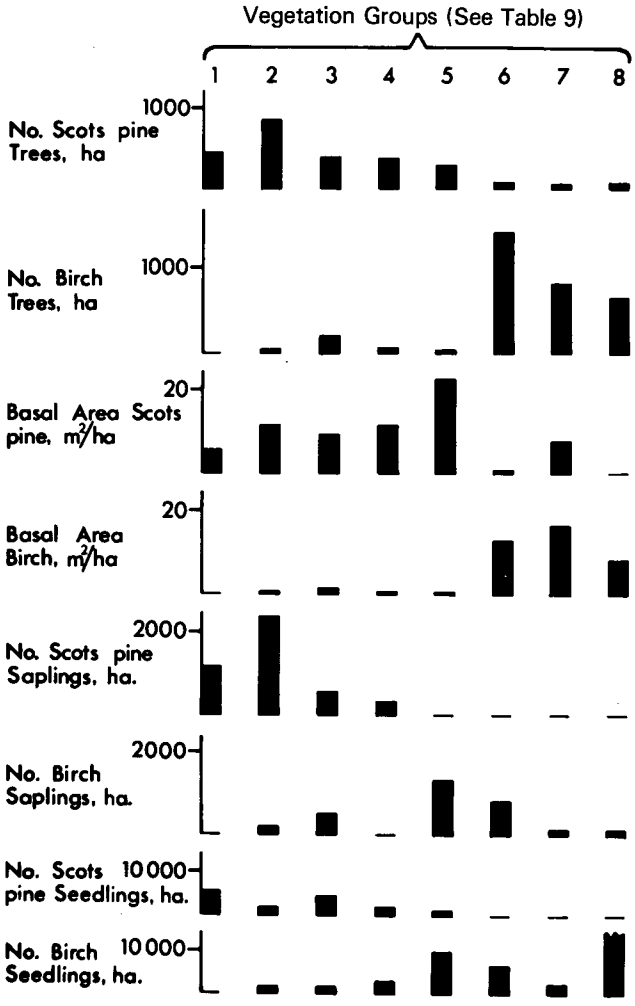

Fig. 18 *Association, at Kirkconnell Flow NNR, between the distribution of sapling and mature specimens of* Betula *spp and* Pinus sylvestris, *and the occurrence of 8 different groupings of other plants.*

created to attract wildfowl, while an arable area of 1.5 ha is left fallow or planted with barley or kale. Because the 'concessions' were expected to increase habitat diversity, attempts are being made to assess the effects of this modified afforestation on the pre-existing vegetation.

The distribution of sampling sites at Stone Chest is, like that at Kirkconnell Flow, based on a regular grid with intersections at 100 m intervals. On the first occasion, in 1972, quadrats were located at 139 sites (Figure 19). The second set of samples, in 1975, was confined to 80 locations whereas in 1978, the third occasion, 87 quadrats were recorded, some having been sampled in 1972 but not in 1975 whereas others had been sampled both in 1972 and 1975. With this sampling method, akin to a partial replacement system, 63 quadrats have been sampled on all 3 occasions.

Ordination has been used as a method for the preliminary examination of changes in the vegetation. Each individual stand is represented as a point in space whose co-ordinates are determined by the species contained in the stand. The first or principal axis along which stands are arranged represents the direction of maximal variation between stands and this is supplemented by other axes which represent other small variations between stands. The arrangement of stands along these axes, which may be expected to reflect environmental gradients, was calculated in this case by using the ordination technique of 'reciprocal averaging' (Hill, 1973). Figure 20 shows the arrangement of stands on the first and second axes of the ordination; each of the re-sampled stands is represented 3 times, one for each sampling occasion, and lines have been drawn between them to show the temporal movement of each stand through the species space of the ordination. In general there is a tendency for stands to have lower scores on the second axis in 1975 and 1978 than in 1972, causing a movement trend down the second axis; on the first axis there is a suggestion of movement from both ends towards the centre. These tendencies are seen more clearly when axes are separated as in Figure 21

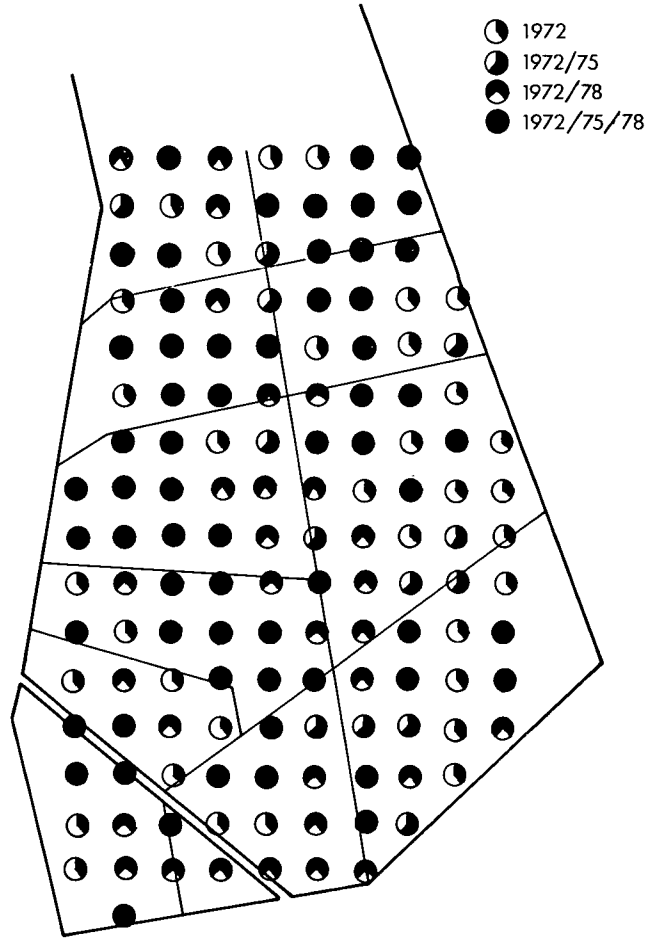

Fig. 19 *Location of sample quadrats, arranged on a 100 m grid at Stone Chest, in 1972, 1975 and 1978.*

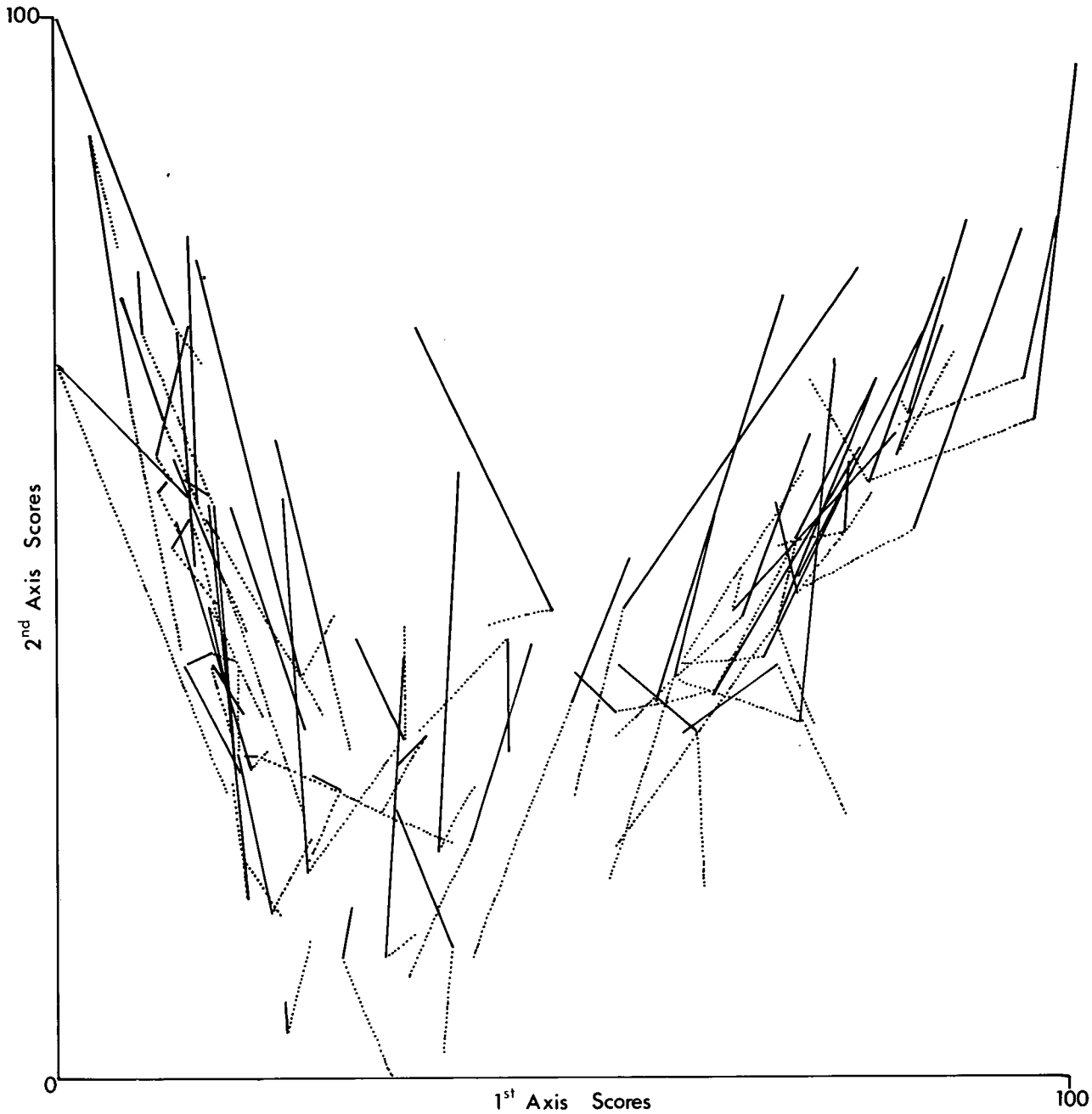

Fig. 20 *Changes in vegetation at Stone Chest, represented by 'movements' on the first and second axes of a reciprocal averaging ordination during 2 periods (1972-5, —, 1975-8, ·····).*

where each line shows the way in which a single stand moved along each of 3 axes during the 2 3-year periods. Stands which had high scores on the first axis in 1972 tended to have lower scores by 1978 and the converse was true of stands with low scores in 1972; those with moderate scores changed relatively little but tended to oscillate. A quite different pattern emerges on the second and third axes, where the overall trend is the same in all stands but is exaggerated in the period 1972-75.

To understand the meaning of these trends requires an interpretation of the meaning of the axes of variation. A step towards explaining their meaning is taken by plotting first axis stand scores against the pH of the 0-5 cm soil horizon (Figure 22). There is seen to be a strong overall relationship between the scores and pH which, when taken together with the time trajectories of the stands on the first axis, suggests that highly acidic soils have decreased in acidity, less acidic soils have become more acidic and those in the middle of the range have been little affected. Classification of the stands into 4 groups based on their first axis scores allows a clearer sight of these different trends (Figure 23). Whilst the mean score of all stands remains constant in time on the first axis, the behaviour of Group 3, which is the most acidic and has vegetation made up of such species as *Calluna vulgaris, Trichophorum cespitosum, Eriophorum angustifolium* and *Vaccinium myrtillus,* is different from Groups 1 and 2, the least acidic which contain species such as *Ranunculus acris, Prunella*

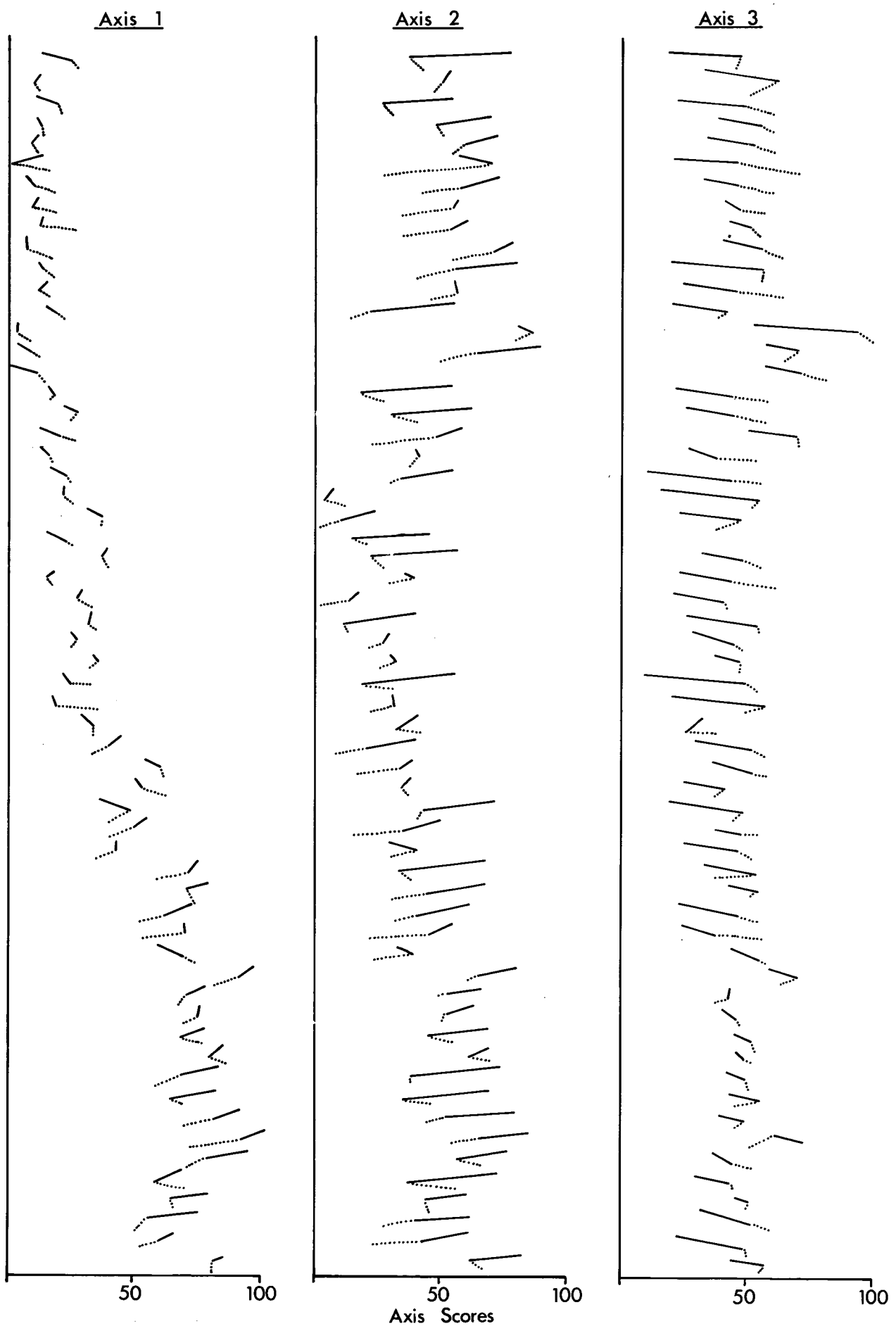

Fig.21 *The extent of change during 1972-5 (–) and 1975-8 (·····) in vegetation assemblages at Stone Chest, when plotted on each of 3 axes of a reciprocal averaging ordination.*

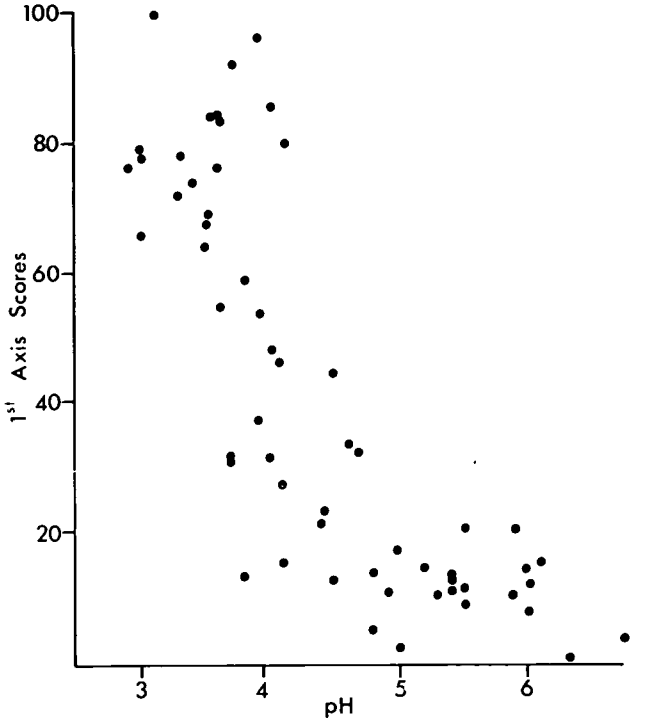

Fig. 22 *Relation between first axis scores from a reciprocal averaging ordination and soil pH in the 0.5 cm soil horizons at Stone Chest.*

vulgaris and *Trifolium repens.* The hypothesis of changing acidity can obviously be tested in the field.

Although the trends of movement by stands along the second and third axes during the 2 time periods are more distinct than those along the first axis, they have not, at this early stage, been fully interpreted because there is no readily measured environmental variable with which they can be correlated. They are likely to be related to a complex of the following factors which have resulted from change in land use at Stone Chest:

(i) Changes in drainage patterns and moisture content of the soil.

(ii) Removal of grazing, enabling some plant species to become dominant at the expense of others which decline or disappear.

(iii) The initial but temporary presentation of new surfaces for colonization resulting from ploughing.

A complete interpretation of the time trends shown by these techniques will depend on an understanding of the species and communities concerned. With only 3 sets of time sequence data available, it is too early to assess the usefulness of this approach in understanding the processes of change, but it appears to be a useful means of summarizing large amounts of data.

Reference

Hill, M.O. 1973. Reciprocal averaging: an eigenvector method of ordination. *J. Ecol.*, **61**, 237-249.

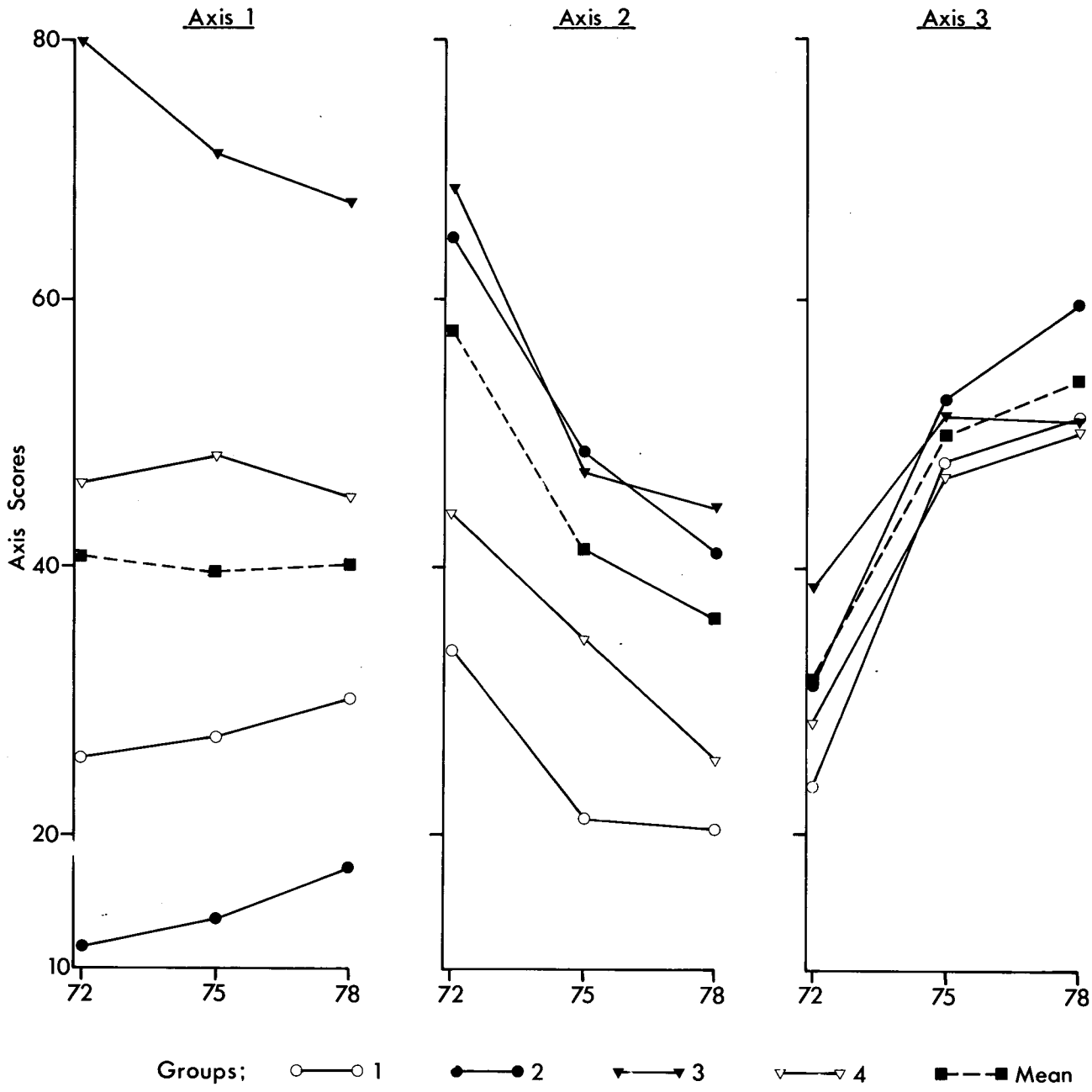

Fig. 23 *Changes in time at Stone Chest in the mean axis scores of 4 vegetation groups.*

8. THE RECOVERY OF GROUND VEGETATION IN COPPICE WOOD: THE SIGNIFICANCE OF BURIED SEED

A.H.F. BROWN

Many of the ancient woods of lowland England have been managed as coppice for hundreds of years. These coppice woods have distinctive, diverse, and ecologically interesting assemblages of plants, some being more-or-less confined to these habitats, eg *Carex pendula, Galeobdolon luteum* and *Oxalis acetosella* (Peterken, 1974). The relatively frequent alternation of light and shade, as a result of coppicing, has favoured the development of a shade flora (including, for example, *Anemone nemorosa, Endymion non-scriptus* and *Mercurialis perennis*), which persists for the whole coppice cycle, and a marginal flora, whose light-demanding species persist in rides and glades. Species of the marginal flora (such as *Cirsium palustre, Lysimachia nemorum* and *Stachys sylvatica*) also recolonise the 'body' of the wood for the first few years after coppicing before being eliminated as shading again intensifies. Salisbury (1924) wrote:

> "The story of the Coppice woods is thus a continual rise and fall in the vigour of the shade flora accompanied by an ebb and flow of the marginal flora. At each coppicing, the latter, as it were, floods the sparsely occupied ground and then, as the shade increases, flows back to its original position".

Because of changing economic and social conditions many coppices have been neglected or have been planted with conifers. As a result, the diversity of the ground flora has decreased, with losses of up to 70% occurring (Table 12), the losses being less in neglected coppice than in woodlands planted with conifers (Brown & Pearce, 1976).

However, to what extent are these changes reversible? It has, for long, been recognised that some recovery of the ground vegetation occurs when neglected coppice is felled; similarly, ground vegetation diversifies as conifer stands age and are thinned, and especially after clear-felling. To what extent does this vegetation represent the original flora? Where do the plants come from? Some will undoubtedly be attributable to the few remaining shade tolerant plants, and others may have immigrated from elsewhere. However, the existence of a seed-bank in the soil might also be of some importance.

1. Experimental observations

It is well known that weed seeds in agricultural soils can persist in a dormant but viable condition for many years (eg Roberts, 1970) or even for centuries (Odum, 1965). Much less is known about dormant seed populations in forest and woodland soils, and most published information refers to North America (eg Kellman, 1970). To gain an insight into the situation in the UK, 27 soil samples were examined from 5 overgrown, neglected coppice woodlands in East Anglia whose current

TABLE 12 Mean numbers, per 200 m^2, of different types of ground flora species found in 11 differently managed East Anglian woods.

Species type	System of managment: Worked Coppice	Neglected Coppice	Coppice planted with conifers
Shade	11.0	8.3 *(75%)*	5.5 *(50%)*
Marginal	13.5	6.3 *(47%)*	3.9 *(29%)*
Woody seedlings	3.6	2.6 *(72%)*	2.5 *(69%)*
Others	1.9	0.8	0.1
Total	30.0	18.0 *(60%)*	12.0 *(40%)*
Species indicative of ancient woodland	3.4	2.5 *(74%)*	1.0 *(29%)*

(Percentages refer to comparisons with worked coppice)

vegetation had already been surveyed. Samples were taken at random from heavily shaded areas in which ground cover was either absent or consisted of *Endymion non-scriptus* or *Mercurialis perennis* and occasional *Rubus fruticosus, Anemone nemorosa* or *Lonicera periclymenum.* Litter and humus layers were discarded from each 30 cm x 30 cm sample area, before collecting the underlying soil, separated into 2 horizons, 0-5 and 5-15 cm below ground level. Subsequently, the soils were transferred to plastic seed-trays in an unheated glasshouse, allowing germination and hence the subsequent identification, of the buried seeds. Although the trays were retained for 30 months, most seedlings had emerged within 2-3 months. Mean numbers of seedlings per tray ranged from 130 to 178 at Chalkney/Weeley and Felsham respectively (Plate 9).

In total, 68 different plant species germinated. For individual woods, numbers averaged 31 with 24 and 23 occurring in the 0-5 and 5-15 cm soil layers respectively (Table 14).

The seedlings that emerged were classified into 3 categories (i) light-demanding species, and those tolerant of (ii) some or (iii) heavy shade, accounting for 87%, 6% and 7% respectively of the total of 8073 (Table 15). The viable seeds were not representative of the current ground flora of neglected

TABLE 13 Mean numbers of seedlings germinating in 2 horizons of soil taken from neglected coppices at 5 sites in East Anglia

Name of Wood	Nos. of replicate samples at each site	Soil horizons, cm below ground level	
		0-5 cm	5-15 cm
		(numbers of seedlings per 4,500 cm^3 of soil)	
Chalkney	6	178	83
Weeley	7	104	155
Felsham	4	181	174
Groton	4	185	128
Parkhall	6	203	133
Combined Woods	27	166	133

Some seedlings emerged in all trays, numbers in surface (0-5 cm) soil averaging 166, equivalent to 1844 m^{-2} or 18.4 million ha^{-1} compared with 133 per tray at a depth of 5-15 cm (Table 13). coppice which consists predominantly of deep-shade species, with a few marginal species. In contrast, the soil seed-bank contains mainly marginal species, but very few species of deep-

TABLE 14 Total numbers of plant species emerging from different soil horizons taken from 5 neglected coppices in East Anglia.

Name of Wood	Soil horizons, cm below ground level		
	0-5 cm	5-15 cm	0-15 cm ie the 2 horizons combined
Chalkney	32	31	41
Weeley	23	20	28
Felsham	19	24	27
Groton	23	13	26
Parkhall	24	27	34
Total nos. of species for all woods, combined	61	57	68
Average no. of species per wood	24	23	31

TABLE 15 Numbers of seedlings of different species (grouped according to shade tolerance) emerging after keeping soil samples from 5 neglected coppices in East Anglia for 2 years in an unheated glasshouse. (Nos. of seedlings from 27 replicate 30 cm x 30 cm samples)

	No. of seedlings		No. of seedlings
Light-demanding species			
Agrostis canina	113	*Plantago major*	1
Agrostis stolonifera	327	*Polygonum aviculare*	1
Anthoxanthum odoratum	105	*Polygonum convolvulus*	23
Betula sp	1335	*Polygonum lapathifolium*	1
Carex pallescens	71	*Polygonum nodusum*	2
Carex pilulifera	50	*Polygonum persicaria*	1
Centaurium erythraea	11	*Ranunculus flammula*	6
Chenopodium album	39	*Rumex obtusifolius*	26
Cirsium palustre	28	*Sagina procumbens*	11
Digitalis purpurea	276	*Salix* sp	4
Epilobium adenocaulon	42	*Sarothamnus scoparius*	2
Epilobium sp	10	*Solanum nigrum*	34
Festuca sp	34	*Trifolium* sp	1
Gnaphalium uliginosum	1	*Tripleurospermum maritimum inodorum*	1
Hypericum hirsutum	3	*Veronica chamaedrys*	6
Hypericum humifusum	34	*Veronica officinalis*	60
Hypericum pulchrum	20	*Veronica serpyllifolia*	7
Hypericum tetrapterum	54		
Isolepis setacea	68		
Juncus bufonius	139		
Juncus effusus	4205		
Lotus corniculatus	15		
Species tolerant of some shade			
Carex pendula	10	*Ranunculus repens*	8
Deschampsia cespitosa	2	*Rosa* sp	1
Euphorbia amygdaloides	1	*Rubus idaeus*	9
Fragaria vesca	3	*Sambucus nigra*	11
Holcus lanatus	26	*Scrophularia nodosa*	4
Luzula pilosa	19	*Silene dioica*	18
Lysimachia nemorum	57	*Solidago virgaurea*	1
Poa nemoralis	5	*Stachys sylvatica*	1
Poa trivialis	27	*Stellaria media*	1
Potentilla sterillis	8	*Veronica montana*	45
Species tolerant of heavy shade			
Ajuga reptans	32	*Primula vulgaris*	3
Carex remota	14	*Rubus caesius*	1
Carex sylvatica	1	*Rubus fruticosus*	446
Corydalis claviculata	13	*Viola* sp	16
Moehringia trinervia	33		

shade; *Endymion non-scriptus, Anemone nemorosa, Lonicera periclymenum, Circaea lutetiana* and *Mercurialis perennis* are notable absentees.

This lack of correspondence between the buried seeds and the current composition of the vegetation is not unusual (eg Harper, 1977). However, it calls into question the origin of the seed-banks: have they survived from the vegetation of an earlier more open phase, or have they immigrated from elsewhere? The evidence supports the former alternative, with some seeds remaining viable for the 30 or 40 years since the woods were last coppiced. Seeds of many species of open, unshaded habitats have (or acquire) a requirement for light in order to germinate—thus remaining dormant while buried. In contrast, seeds of species of closed vegetation (including the shade species of forests), although possibly requiring a chilling or other pre-treatment, seem to germinate equally readily

in light or dark conditions (Grime & Jarvis, 1975), and are therefore not incorporated into the seed-bank. The paucity of shade species in seed-banks in coppice woods matches observations on North American (Leavitt, 1963; Kellman, 1974) and on Russian forest soils (Karpov, 1960).

2. Implications

Traditionally, it has been considered that the marginal flora of coppice woodlands would reinvade freshly cut areas by its spread from rides and glades (Salisbury, 1924; Rackham, 1975). However, there is increasing evidence (Brown & Oosterhuis, 1981) that this ebb and flow, in the sense of retreating to, and re-invading from, open areas is of less importance than the buried seed-bank. If this is an effective mechanism where trees are coppiced, there seems to be no immediate reason why it should not also apply when old coppice is converted to conifers, although the longer rotation of conifers (50 yr), compared with the coppice cycle of say 15 years, may well eventually reduce seed survival. Preliminary studies indicate that seeds of a similar range of species survive in soils of 20 year old coniferous plantations (Brown, 1979).

In contrast, not only do the deep-shade species seem to be absent from the soil seed-bank, but other evidence (Webb, 1966) suggests that their migration from elsewhere is likely to be slow; they tend to produce relatively few but heavy seeds which remain close to parent plants (Salisbury, 1942), unless spread by animals such as ants (Ridley, 1931; Fahn & Werker, 1972).

In summary, it seems that:

(i) marginal species and species of less extreme shade are able to survive in soil-borne seed-banks for periods of 30 years or more, and thus have the potential to recover, and (ii) species of deep-shade, if lost because of extreme conditions, eg the seasonally unvarying intense shade in evergreen coniferous plantations (compared with the seasonally variable shade in stands of deciduous trees), will only be re-established with difficulty, if at all.

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9. THE CONSERVATION OF PASTURE-WOODLANDS

P.T. HARDING

In Britain the conservation of woodlands has been directed mainly towards those woods with rich and diverse arrays of seed-bearing plants, or towards presumed examples of vegetational types. Recently, however, the desirability of conserving woodlands whose structure has been determined by different types of management was emphasised by Peterken (1974, 1977*a, b*). Five types were recognised by Peterken:

a) Relicts of the medieval wood–pasture systems, [pasture-woodland] ;

b) Ancient high forest woods, ie the native pinewoods of Scotland and some birchwoods in the highlands;

c) Ancient coppice woodlands;

d) Ancient woods in inaccessible sites;

e) Woods formed by a long period of natural structural development.

Of these, ancient woods managed as coppice or as high-forest, or on inaccessible sites, make up most of the areas considered to be of value for wildlife conservation.

Examples of wood-pasture (pasture-woodland) management are of particular importance because, although relatively few areas are still managed in the traditional manner, many retain the associated structural features, characterised by the presence of over-mature broadleaved trees and dead wood, which are not commonly found in areas of woodland managed in other ways, for example high forest or coppice. The structure of broadleaved trees, particularly oaks *(Quercus robur* and *Q. petraea),* beech *(Fagus sylvatica),* ash *(Fraxinus excelsior)* and elms (*Ulmus* spp), in open canopy over grassland or bracken, frequently with areas of scrub, especially hawthorn *(Crataegus monogyna),* typifies pasture-woodlands. Pasture-woodlands were managed from pre-Norman times to provide grazing for deer and domestic stock, the tree component yielding both timber, winter shelter and food for deer and stock. Although areas of pasture-woodland have decreased since the late Middle Ages, they are thought to have survived better in lowland Britain than elsewhere in western Europe. Four broad types of pasture-woodlands are discernible: forests and chases, parks, wooded commons and winter grazed woodlands (Rackham, 1976; Rose & Harding, 1978).

Areas of pasture-woodland were recognised in the Nature Conservation Review as being important, particularly for the conservation of epiphytic lichens, timber-utilising invertebrates and hole-nesting birds (Ratcliffe, 1977).

1. The characteristic natural history of pasture-woodlands

Many species of coleopterous and dipterous insects occur in woodland, but some, such as *Bitoma crenata, Pediacus dermestoides* and *Litargus connexus,* are largely restricted to pasture-woodlands. Many of these restricted species are associated with dead or dying trees, itself a rare ecological resource (Stubbs, 1972). However, species such as *Abreus granulum, Ampedus cardinalis, Ischnomera sanguinicollis, Phloiotrya vaudoueri, Ptenidium gressneri* and *Rhizophagus oblongicollis* and some assemblages of species seem to be restricted further and occur only at sites known to have been managed as pasture-woodland for many centuries or throughout their recorded history. These species are comparable with the Urwaldtiere of "Old Forest Insects" of Palm (1959) and Buckland and Kenward (1973).

A preliminary list of 195 such species of Coleoptera has been compiled (Harding, 1977*a*) and a bibliography of the occurrence of 100 of these species in the British Isles (Harding, 1978*f*) is being used by a number of entomologists to evaluate the usefulness of such a list for conservation assessment purposes (eg Hammond, 1979).

Similarly, some assemblages of lichens and bryophytes such as the *Lobarion pulmonariae* community, can be regarded as characteristic of pasture-woodlands and to be indicative of ecological continuity (Rose, 1974, 1976; Rose & Harding, 1978; Rose & James, 1974; James *et al.,* 1977).

2. The extent of areas of conservation value

The Nature Conservancy Council wanted an up-to-date assessment of the extent and condition of the national resource of pasture-woodland habitats. ITE was commissioned to make a survey to enable this assessment to be made, and also to facilitate the evolution of improved management. The survey concentrated on invertebrates associated with dead wood, but with the occurrence of cryptogams being noted. With information from many entomologists and botanists, local conservation and natural history organisations, NCC staff, and colleagues in ITE, an annotated and slightly revised version of an earlier inventory (Harding, 1976) was prepared. This revision includes more than 400 areas considered to be of possible,

TABLE 16 Dynevor Deer Park, Dyfed: Age classes and growth forms of broadleaved species of trees and shrubs

	ANCIENT	OVER-MATURE		MATURE		YOUNG						
	Maiden	Pollard	Maiden	Pollard	Maiden	Maiden	SAPLING	SHRUB	COPPICE	BOLE ONLY	DYING/DEAD	TOTALS
OAK *(Quercus robur & Q. petraea)*		57	488	4	243	4				4	19	819
ASH *(Fraxinus excelsior)*		1	8		11	4	4				4	32
ELM *(Ulmus glabra)*		3	3	1	3	1	2		3	1	26	43
ELM *(U. carpinifolia)*					2							2
BEECH *(Fagus sylvatica)*		6	34	2	28	2	3		1	1	5	82
LIME *(Tilia x vulgaris)*		2	5	2	18	8						35
ALDER *(Alnus glutinosa)*						1	2					3
BOX *(Buxus sempervirens)*								3				3
HAZEL *(Corylus avellana)*								9				9
SALLOW (*Salix* spp)											1	1
ELDER *(Sambucus nigra)*											1	1
HOLLY *(Ilex aquifolium)*					1		3					4
HAWTHORN *(Crataegus monogyna)*								20				20
RHODODENDRON *(R. ponticum)*								21*				21*
SYCAMORE *(Acer pseudoplatanus)*		1	30	5	63	7	7				1	114
OTHER MAPLES (*Acer* spp)		1	3	1	3	1						9
HORSE CHESTNUT *(Aesculus hippocastanum)*		5	3	6	12	19			1		2	48
SWEET CHESTNUT *(Castanea sativa)*	2	2	13	2	7	1					1	28
CHERRY (*Prunus* spp)						3						3
WALNUT *(Juglans regia)*					1					1		2
TURKEY OAK *(Quercus cerris)*				2	12						1	15
HOLM OAK *(Quercus ilex)*					3							3
TOTALS	2	78	587	25	407	51	21	53	5	7	61	1297

* Isolated shrubs only. Two dense areas of shrub are also present.

potential, or known conservation value for "the fauna of the mature timber habitat" (Harding 1978*e*)—the assessment being based on knowledge of invertebrate faunas, the structure of woodlands and historical records.

3. Surveys

Approximately 100 areas were surveyed between 1975 and 1978 to include a wide geographical range, with some areas which were known for their entomological interest and/or abundance of epiphytes together with hitherto unrecorded areas (Harding, 1976, 1977*a*, 1978*a-d*).

At each site, 5 attributes were recorded to give a brief assessment of the present-day appearance and management of the site.

3.1 Species composition, and species ratio, of trees and shrubs. Oak and beech were usually the most plentiful tree species, but birch, ash and elm were also frequent. Exotic species such as sycamore and sweet and horse chestnut were frequent where landscape plantings had been made in the 18th and 19th centuries. Hawthorn occurred at almost every site, but at many sites shrubs were scarce.

3.2 Age classes of trees and shrubs. Most sites were characterised by an abundance of overmature trees (fully grown trees with dieback affecting some branches in the crown) and a lack of young trees (actively growing trees not yet having reached the presumed maximum in height and spread of crown). Table 16 shows a typical example of the age class structure of a parkland pasture-woodland in lowland Britain.

3.3 Regeneration/planting of trees and shrubs. Except where deer and other grazing stock were no longer present, successful natural regeneration of trees and shrubs was rare. Planting was infrequent except in a few cases, such as some National Trust properties (eg Dunham Massey Park in Greater Manchester) and a few privately or municipally owned parks, where small "cosmetic" plantings had been made in recent years. At most sites, the most recent phase of regeneration or planting

seemed to have been before the end of the 18th century (Plate 10).

3.4 Estimates of the amount and distribution of dead wood and the "fate" of dead wood. At most sites, dead wood was cleared either for firewood or to free land for grazing, or, as at Cadzow in Strathclyde, apparently to achieve a tidy appearance, or, in public access areas, in the interests of safety. Few examples of areas of relatively undisturbed dead and dying trees and fallen branches, as at Staverton Park in Suffolk, were found.

3.5 Present management and prospects. The management of most parkland sites was organised towards achieving the maximum amount of grazing on the land without completely destroying the characteristic appearance of parkland.

Many parks acted as a dual source of grazing for stock and deer, and of shooting, usually, as at Moccas Deer Park in Hereford/Worcester, as a properly keepered pheasant shoot embracing an area much larger than the park itself. Other parks have been opened up to public access as safari parks (eg Longleat in Wiltshire) or as public recreation areas (eg Studley Royal Park in north Yorkshire). A few sites had been ploughed and most of the trees removed in recent years. Most of the former forest and chase areas are now managed for commercial forestry which has resulted in a loss of old trees. Although young trees have been planted at these sites, they are frequently of species not readily available as hosts to the typical flora and fauna of native broadleaved species. Two important forest areas, Epping Forest in Essex, and the Birklands area of Sherwood Forest in Nottinghamshire, are intensively used by the public for recreation. It is probable that these areas, together with parts of the New Forest in Hampshire, will experience new problems resulting from damage, particularly by fire and vandalism, by the public in the future.

Detailed surveys of 6 sites have also been made. The primary objective of each survey was to locate, map, identify to species and allocate to an age class and growth form, each tree and shrub at the site. From this information it was possible to state the present age structure for each species of tree and shrub (eg Table 16) and to propose what management would be necessary to maintain and, if possible, to enhance the value of the site for the conservation of timber-utilising invertebrates and epiphytes. In all cases, extensive programmes of planting were proposed, and, in some cases, it was recommended that small enclosures should be made to aid natural regeneration. The retention of dead wood, a highly valuable wildlife resource (Stubbs, 1972), was a recurrent problem at these sites. In one case, it was recommended that a few particularly important dying and dead trees be purchased by NCC at their timber (firewood) value to ensure their continued presence to act as hosts for invertebrates. At Moccas Deer Park in Hereford/Worcester the detailed report of the structure, natural history, management and history of the park (Harding, 1977*b*) has been used by the Nature Conservancy Council (West Midlands Region) in its attempts to obtain a Nature Reserve Agreement. This is expected to be formally agreed in 1979, although the management recommendations are already being implemented.

4. Conclusions

The results of various surveys of pasture-woodlands, made by ITE staff between 1975 and 1978 have been reported to NCC. In some cases, recommendations about the value of sites for the conservation of invertebrates and epiphytes associated with old trees have been acted upon by NCC. However, unless concerted action is taken to manage at least a representative set of sites for wildlife conservation, an important and little understood facet of woodland ecology in Britain will be seriously damaged or permanently lost, mainly as a result of neglect.

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Tree physiology and the influence of the physical environment

10. SITE FACTORS INFLUENCING THE GROWTH OF STANDS OF SCOTS PINE IN GREAT BRITAIN

E.J. WHITE

With the realisation that supplies of fossil fuels are not limitless, it becomes increasingly important to understand the factors that control growth and transform solar energy, moisture and nutrients into wood, possibly a continuously renewable fuel. For this purpose, and hoping that it would be possible to devise ways of increasing "efficiency", possibly by changing silvicultural practices, a study was made of the growth of Scots pine, *Pinus sylvestris,* analysing the relations between growth and site variables by using principal component analyses and orthogonalized regressions.

Comparable studies have already been made of Sitka spruce by Mayhead and Broad (1978) and Malcolm (1976); of Sitka spruce, Douglas fir and Japanese larch by Page (1970). These workers, like students working with Scots pine in the Soils Department of the University of Aberdeen, found that elevation was of major importance. However, in analyses of Corsican pine, *Pinus nigra* var. *maritima,* Fourt *et al.* (1971) found that evapotranspiration during summer was the dominant factor, although, in their analyses, this factor incorporates (confounds) the effects of altitude at least to some extent. In the study made by Fourt *et al.*, growth of Corsican pine was found also to be significantly related to soil chemical and physical characteristics but these characteristics were not of primary importance. Because these studies were made of different tree species growing in restricted parts of the UK, it was decided to extend the approach to sites throughout the country. Would principal component analyses and orthogonalized regressions be as effectively discriminating when applied to stands distributed throughout the UK? As it has been widely planted, with Forestry Commission sample plots distributed in most of the afforested parts of the UK, it was decided to assess the growth of Scots pine.

1. Methods

During the summer of 1975, 101 variables, arranged in 11 groups (White, in prep.), were recorded at each of 73 sites (Figure 24):

1.1 Dependent variable

Size and age of *P. sylvestris.* Because stands of *P. sylvestris* can progress from one yield class to another within the span of a rotation, this fairly coarse dependent variable was replaced by 'Y', a term expressing the relation between actual growth and that predicted from the relation between $\log_e$ Top Height (m) and $\log_e$ Age (yrs):—

$$\log_e (\text{Top Height} - 10.0) = 0.584 \log_e (\text{Age} - 27.0) + 0.285 \quad 1)$$

where Top Height = mean height of the 100 largest trees ha^{-1} as assessed from diameters measured 1.3 m above ground.

1.2 Regressor variables

a) Geographical—latitude and longitude

b) Topographical—elevation, slope and aspect

c) Competition—type and intensity of thinning

d) Total soil depth

e) Physical properties of top 5 cm of soil

f) Physical properties of soil 5-25 cm below ground level

g) Chemical properties of top 5 cm of soil

h) Chemical properties of soil 5-25 cm below ground level

NB The physical and chemical soil variables were similar to those assessed in other studies with the addition of extra variables coping with the estimation of soil phosphorus.

i) Monoterpenes—Because trees from different seed-lots grow differently, an attempt was made to identify genetical affinities by assessing the balance of monoterpenes, a supposedly distinctive and unvarying marker, in resin taken from needles.

j) Climate—temperatures, rainfall, visibility, indices of wind direction and snow depth were calculated from equations given by White (1979), knowing latitude, altitude and other map readable site characteristics.

Although it was deemed necessary to include a large number (101) of site variables to ensure that

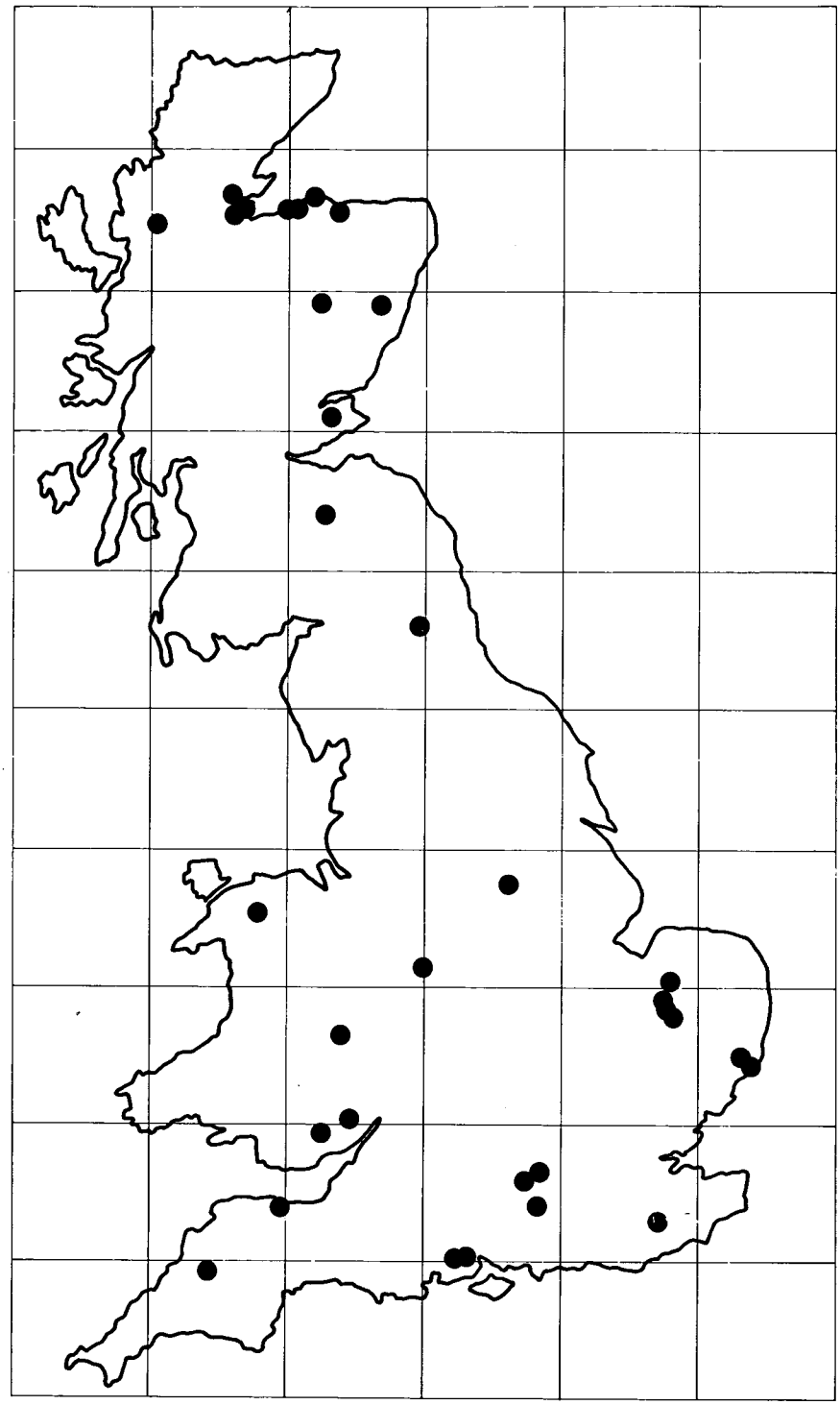

Fig. 24 *Map showing the distribution in England, Scotland and Wales of Forestry Commission Scots pine sample plots studied during 1975.*

important factors were not overlooked, it was equally important to effect simplification as soon as possible. This was done by principal component analyses (PCA) applied to 3 sets of site variables including chemical and physical soil variables expressed in:

(i) quantities per unit soil weight

(ii) quantities per unit soil volume allowing for stones and bulk density

and (iii) quantities per profile as for (ii) but allowing for depth

After calculating orthogonalized regressions, it was found that tree growth was more closely related, as judged by the amount of associated variation, to soil variables, including nutrients, expressed per unit soil volume than to the other 2 data sets. By setting aside data sets (i) and (iii) the dependence of tree growth, designated 'Y', was estimated by a complex of step-up multiple regressions on regressor variables starting with those selected by PCA (See method B4 of Jolliffe (1972) (Figure 25). As a result, 2 equations were obtained. In one, growth of Scots pine was related to 7 regressor variables, each of which accounted for a statistically significant amount of variation and in the other to 17 variables, the 7 plus 10 others which together minimized the standard deviation from the regression (Snedecor & Cochran, 1967).

2. Results

The 7 statistically significant variables were:

Variable	Cumulative percentages of variation explained
Mean summer solar radiation from July to September, measured at ground level	30.1
Silt, % vol, in top 5 cm of soil	35.5
Stones, % vol, in soil 5-25 cm below ground level	42.4
Moisture content of soil, 5-25 cm below ground level (% vol of air dry soil)	47.3
Index of mean wind direction July-Sept (degrees)	51.3
Log_e of the water holding capacity of top 5 cm of soil (% vol)	53.6
Distance from sea x slope to west (km), an index of 'exposure'	56.8

The additional 10 variables to minimize the standard deviation of the regression included "expressions" of soil phosphorus, including isotopically exchangeable phosphorus, topography and additional aspects of soil texture and water holding capacity.

Not surprisingly, growth of Scots pine was closely and directly related to solar radiation (energy), a factor not previously identified in other research no doubt because of the unavailability of solar radiation maps first made available by the Meteorological Office in 1976. However, there were distinct differences in different parts of the country with variations in amounts of solar radiation being relatively unimportant within the north-east region of Scotland, Wales and south-west England, and south-east England including East Anglia.

After solar radiation, the next most generally important factors were those concerned with soil physical properties, growth being directly related to water holding capacity and increasing concentrations of silt and stones, and amounts of moisture (Figure 26).

In the north of Britain, growth was related to the shape of the contours, passing through the sample plots, from which effects on shelter and percolation down slopes were inferred, whereas in the south, summer soil moisture at 5-25 cm below ground level was an important factor. In the south-west a significant relation with monoterpenes suggests that the growth of Scots pine varied considerably with origin, an effect not noticed elsewhere.

3. Discussion

Because different research workers have used distinctive variables, many of which integrate the effects of a variety of associated factors, it would be unwise to overemphasize differences between the results of their analyses. However, in the present analyses, done for most of the UK and in which estimates of solar radiation were included, elevation did not prove to be a statistically significant factor affecting the growth of Scots pine. However, in analyses made of Scots pine in a restricted part of the Scottish uplands, students at Aberdeen University found, without the inclusion of solar radiation data, that elevation was of major importance, an observation which is not in conflict with the results given in this paper. In additional analyses restricted to the north-east, amounts of solar radiation were found to be independent of elevation and in this circumstance a topographical variable relating forests to either valleys or hill-tops was of significance in addition to soil depth and mean wind speed during April-June.

Although the opening and closing of Sitka spruce stomata are critically related to changes in atmospheric saturation vapour deficits (Watts *et al.*, 1976; Jarvis & Stewart, 1979), macroscopic growth was

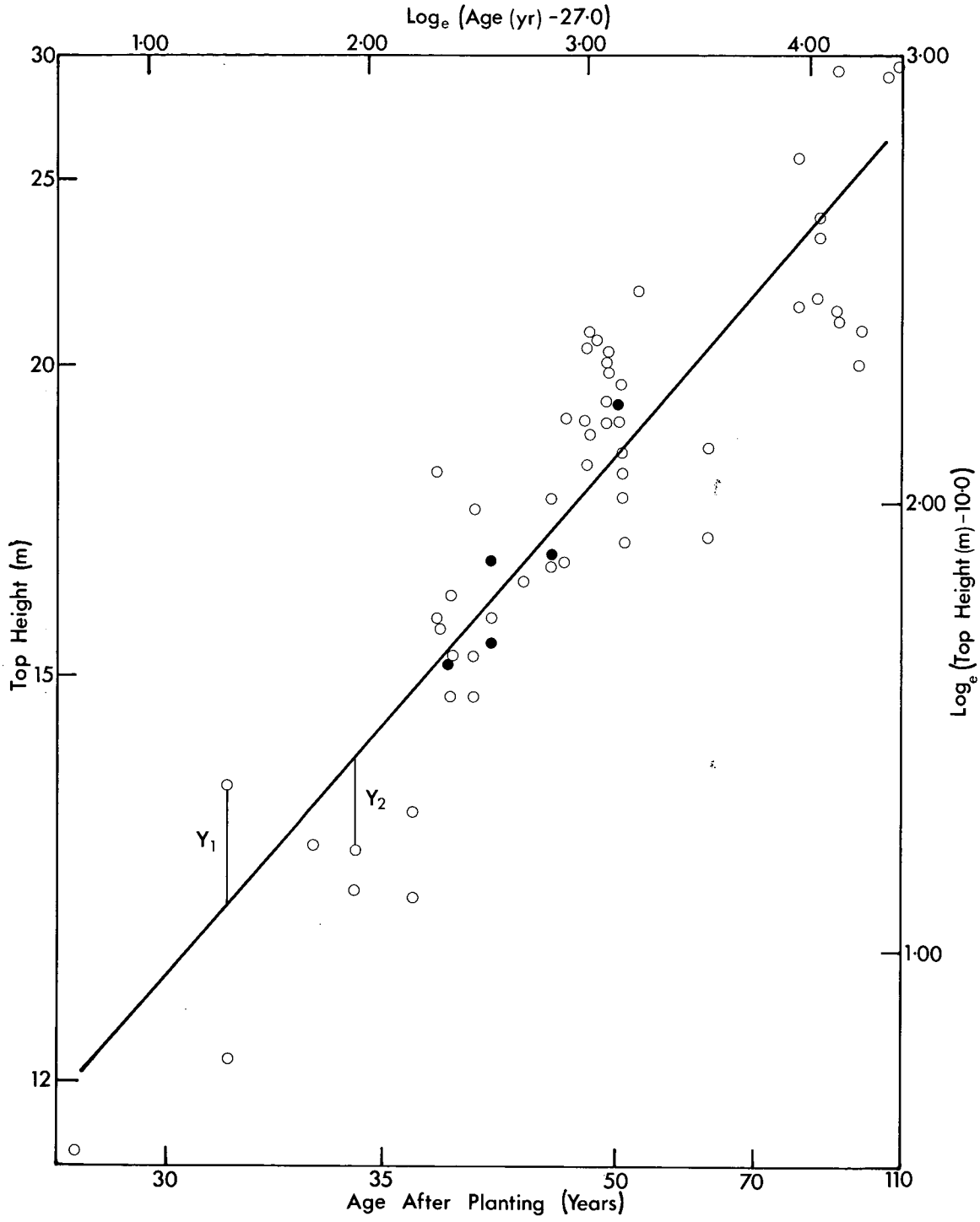

Fig. 25 *Relation between (i) top height (m) and (ii) age, in years after planting, of Scots pine grown in sample plots at many different locations in the UK. The lines Y_1 and Y_2 indicate the deviations between actual and predicted heights of stands of trees about 31 and 34 years old respectively.*

less stringently related to available soil moisture (Malcolm, 1976) than might have been expected. On the other hand, the guard cells of Scots pine stomata seem less sensitive to stress than those of Sitka spruce yet there was a strongly positive relation between the growth of the former and amounts of soil moisture.

Although growth differences in different parts of the UK were not attributable in the present analysis to temperature variations—in the north-east of Scotland, the predicted quarterly mean air temperatures were strongly and negatively correlated with altitude—they were in an analysis restricted to trees in the nothern Pennines (White, 1974). Here, Scots pine was particularly responsive to soil temperatures from May to early August. Although the relation between predicted air temperatures (April-June) (T_2) and growth (Y) in the analysis described in this paper was inexact it

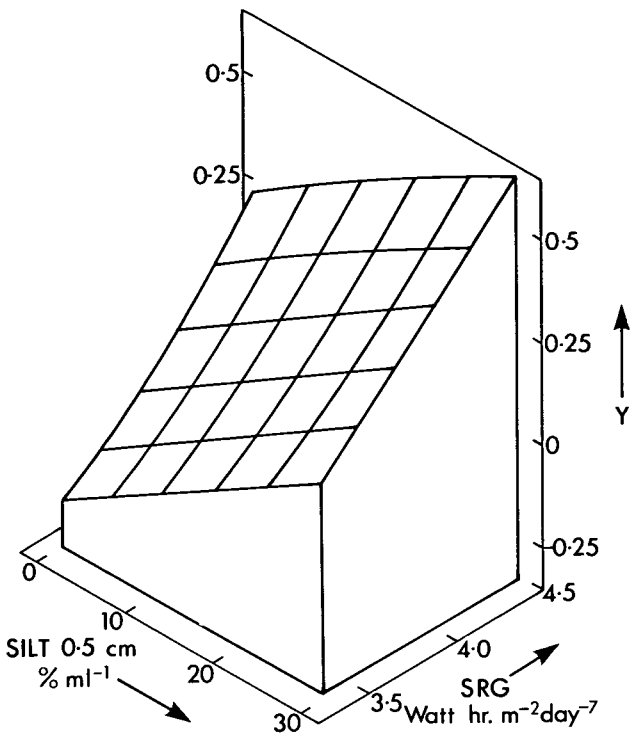

Fig. 26 *Relation between predicted height growth rate of Scots pine (expressed as deviations from equation 1) (Y), and (i) concentrations (% ml^{-1}) of silt in the top 5 cm of soil, and (ii) the mean incoming solar radiation at ground level (SRG) from July to August (Watt hr. m^{-2} day^{-1}).*

was nevertheless statistically significant at p=0.01:

$$Y = 0.766\,T_2 - 0.824 \qquad 2)$$

This equation suggests that a climatic deterioration of 1°C from the April-June mean would be associated with a top height decrease in trees, 50 years old, of 0.6 m from 18.3 to 17.7 m. This loss of height would be reflected in a 7.3% decrease in accumulated volume growth (Hamilton & Christie, 1971).

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11. THE ROLE AND USE OF WATER IN SITKA SPRUCE PLANTATIONS

R. MILNE

Rain falling on a forest can be partitioned into 3 major components:

Throughfall—the fraction falling on ground directly or dripping from branches

Stemflow—the part collected on branches and running to soil via tree trunks

Interception—the fraction trapped on branches and needles and evaporated back to the atmosphere.

Water reaching the ground either flows to streams and rivers, Runoff, or is taken up through plant roots and foliage, passing through stems into the Transpiration stream.

It goes without saying that the partitioning of rainfall can greatly affect plant growth, and that the use of water influences the effects of afforestation on the water budgets of upland catchments. Ford & Deans (1978) and Deans (1979) found that patterns of root growth reflected changes, both in time and space, of soil moisture, and there are indications that the internal availability of water may affect shoot and cambium growth of trees.

The results will be considered in relation to:

i) Transpiration and the partitioning of rainfall.
ii) Internal moisture stress.

1) Transpiration and rainfall partitioning

The theory of transpiration and evaporation has been well argued (eg Jarvis & Stewart, 1978) but it needs to be validated by greater numbers of experimental measurements of water loss from differing forest sites. Staff of ITE have concentrated on the measurement of transpiration from the dry canopy of Sitka spruce planted in 1962 at Rivox Moor within Greskine Forest. The investigation has exploited the development of energy balances and techniques, the use of the eddy correlation method to estimate the flux of latent heat and thence the canopy resistance to water loss from stomata, assessments being made during periods of 6 days in 1976 (Milne, 1979) and 1978.

In a forest, with a constant canopy temperature, energy from the sun is partitioned into 3 fractions, those (a) going into the soil, (b) lost in the transpiration stream and (c) lost as a sensible heat flux by the turbulent convection of warm air. Thus latent heat flux (λE) can be estimated from —

$$\lambda E = R_N - G - H \qquad (1)$$

where R_N = net radiation
G = soil heat flux
H = convective or sensible heat flux

H, the sensible heat flux, was estimated using the eddy correlation method (Dyer *et al.*, 1967)

$$H = \rho c_p \overline{w'T'} \qquad (2)$$

Where ρ and c_p are the density and specific heat of air respectively, W is the vertical wind speed and T is air temperature.

The bar above w' and T' denotes a time average and the prime, as in w', a deviation from the mean.

Vertical wind speed was measured by a horizontally mounted Gill anemometer and air temperature by a fast response beam thermistor both of which were 2 m above the 7 m tall forest. The outputs of the anemometer and thermistor were connected to a 'Fluxatron' circuit (Hicks, 1970) which produced a signal proportional to instantaneous sensible heat flux. This signal was averaged over periods of 20 minutes by an analogue/digital circuit, the averages then being recorded with a computer controlled data logger.

Transpiration from a dry canopy is given by the Penman-Monteith equation (Monteith, 1965):

$$\lambda E = \frac{\Delta (R_N - G) + \rho c_p (\delta e / r_a)}{\Delta + \gamma . (1 + r_c / r_a)} \qquad (3)$$

where Δ = the slope of the saturation vapour curve
δe = the vapour pressure deficit of air
γ = the psychrometric constant
r_a = the resistance to transfer of heat or water vapour (assumed to be the same) in the atmospheric boundary layer
r_c = the resistance to transfer of water vapour from canopy (ie net effect of all stomatal resistances)
E = the transpiration as a mass flow
λ = the latent heat of evaporation of water

Using the Bowen ratio, β (=H/λE,) equation (3) can be rearranged to give the following estimate for canopy resistance:

$$r_c = (\beta\Delta/\gamma - 1).\ r_a + (\rho c_p/\gamma).\ (\beta+1).\ (\delta e/(R_N-G)) \quad (4)$$

During an experimental period in July/August 1976 the mean transpiration rate of Sitka spruce was 3 mm/day implying that each of the 4700 trees/ha lost about 6 litres of water daily. Because Ford and Deans (1978) found, when studying the same stand of Sitka spruce, that the average input of rain to soil was about 7.5 litres/tree per day in the period from May to August, it seems that transpiration during these summer months removes most of the rain falling on the ground. When an allowance is additionally made for runoff, there can be no doubt that moisture potentials are likely to fall below -0.17 bar, a potential with which the death of fine roots at Rivox is associated (Deans, 1979).

Generally it was found that changes in rates of transpiration within a day were significantly correlated with radiation changes, a feature confirmed by measurements of shoot water potential. Typically, transpiration was maximal just after mid-day (Figure 27); Bowen ratios ranged from 0.0 to 1.5 with canopy resistance usually cycling from 150 sm^{-1} shortly after dawn to 40 sm^{-1} by early/mid-morning with a return to >100 sm^{-1} by evening (Figure 28).

Comparisons made with published results from other UK sites (Jarvis *et al.*, 1976) suggest that generalisations should not be made about either the response of a single species in different locations or the response of a range of species growing in the same weather conditions, until more is known of the interactions between trees and their forest environments. To this end the use of a null balance porometer was included when assessing stomatal resistance of Sitka spruce needles in an extended collaborative project done in 1978 with Prof. P.G. Jarvis. With this direct method of assessing stomatal resistances it should be possible to check the validity of the estimates obtained indirectly from equation (3).

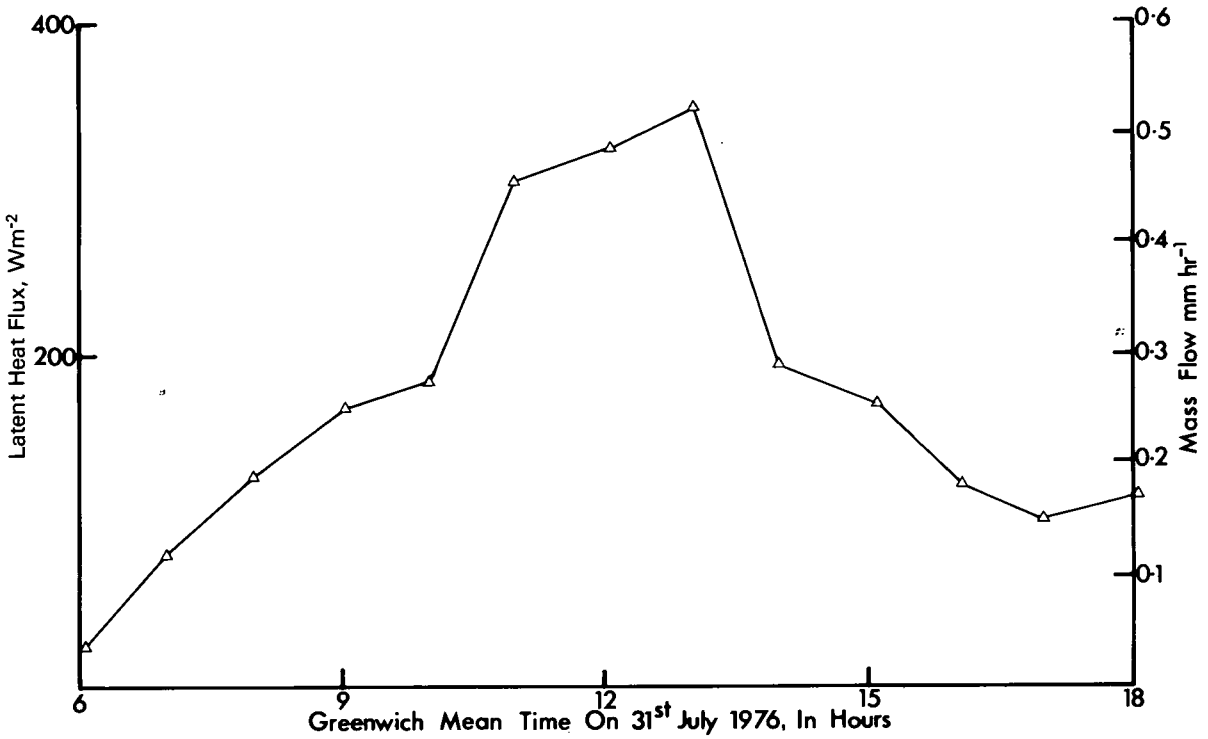

Fig. 27 *The diurnally changing rates of transpiration from a Sitka spruce plantation at Rivox Moor, Greskine forest, Scotland, transpiration being expressed as either latent heat flux or mass flow.*

For the future, it seems that advances will depend, to some considerable extent, on the development of more sophisticated instruments to aid:

a. replacement of existing hybrid systems for calculating average heat fluxes from vertical wind speed and air temperature measurements by an integrated system based on the Rockwell AIM 65 microcomputer using the R6500 chip set;

b. replacement of the Fluxatron propellor anemometer by a simple cheap sonic anemometer which should be more responsive to small eddies thus minimizing the inevitable underestimates incurred at present and possibly

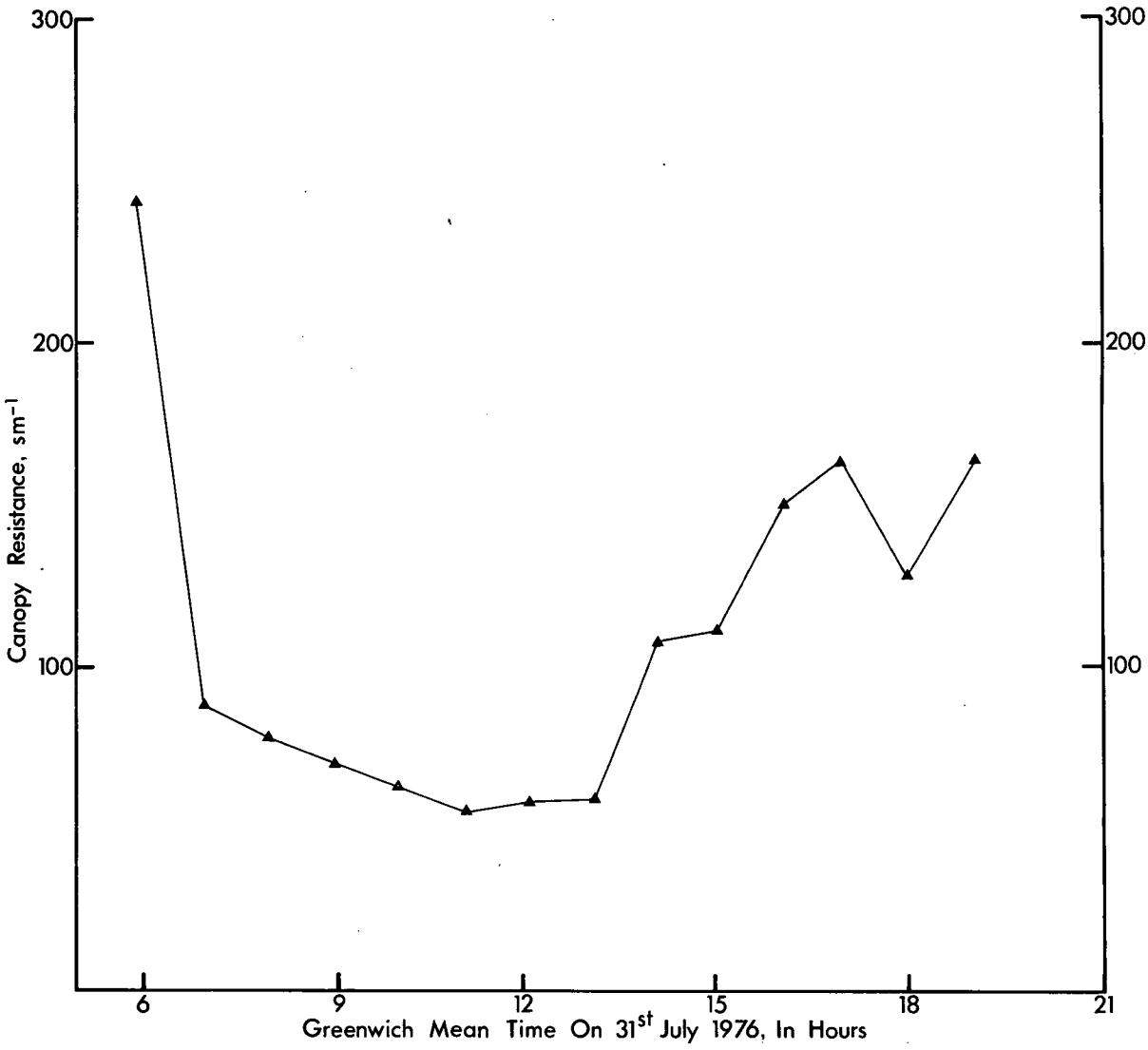

Fig. 28 *Diurnal changes in canopy resistance (r_c) of a Sitka spruce plantation at Rivox Moor, Greskine forest, Scotland.*

responsible for errors of 15% when calculating heat flux;

c. direct measurement of latent heat flux (transpiration) by linking a humidity sensor with the vertical wind speed sensor in the sensing head of the Fluxatron;

d. for measuring rainfall, throughfall and stemflow over short time scales with a resolution of 0.005 mm but able to cope with amounts up to 250 mm per hour. These requirements are necessary because work done on rainfall partitioning by other members of the ITE team (Ford & Deans, 1978) is based on weekly samples which are too coarse to permit either detailed analyses of individual storms or comparisons with published models (Rutter *et. al.*, 1971).

2) Internal moisture stress

Measurements of tree moisture potential, using a pressure bomb, and of changes in stem diameter taken at hourly intervals have been made on a number of occasions, the data subsequently being analysed using discrete difference equation models (Box & Jenkins, 1970). As yet the relation of changing moisture storage, within plant cells, and the physical environment has not been satisfactorily elucidated. More recently, detailed measurements of tree moisture potential and stem diameters have been supported by estimates of canopy water losses using energy balance/eddy correlation methods. The data obtained should enable models of the resistance–capacitance analogue type (Jones, 1978, Landsberg *et al.*, 1976) to be developed, compared with the Box-Jenkins version and hence used in relating transpiration flows in the atmosphere with events actually occurring within trees.

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12. ROOT GROWTH AND ITS RELATION TO THE WATER ECONOMY OF A SITKA SPRUCE PLANTATION

J.D. DEANS

In the UK, most of the plantation forests have been established in the uplands of the north and west, where the annual excess of precipitation (rainfall) over evaporation has typically led to the development of acid peat deposits which remain wet and waterlogged for most of the year. Because of waterlogging in the rooting zone and/or intense root and shoot competition from other plants (the native ground vegetation), the early methods of direct transplanting of young trees into wet peat were found to require modification if poor growth and crop failures were to be averted (Zehetmayr, 1954). Thereafter, different ploughing techniques have been used where single or double mouldboard ploughs throw up, and invert, ribbons of peat, normally aligned downslope, so that parallel strips are spaced 1.5-2.0 m apart. As a result, a structure (planting unit) of shallow ditches and raised ridges is produced with the inverted turf sandwiched between undisturbed and inverted peat (Figure 29). This structure helps regulate water movement, increase soil aeration and decrease competition from the ground vegetation (Taylor, 1970). At intervals, the shallow ditches are linked to deeper cross drains.

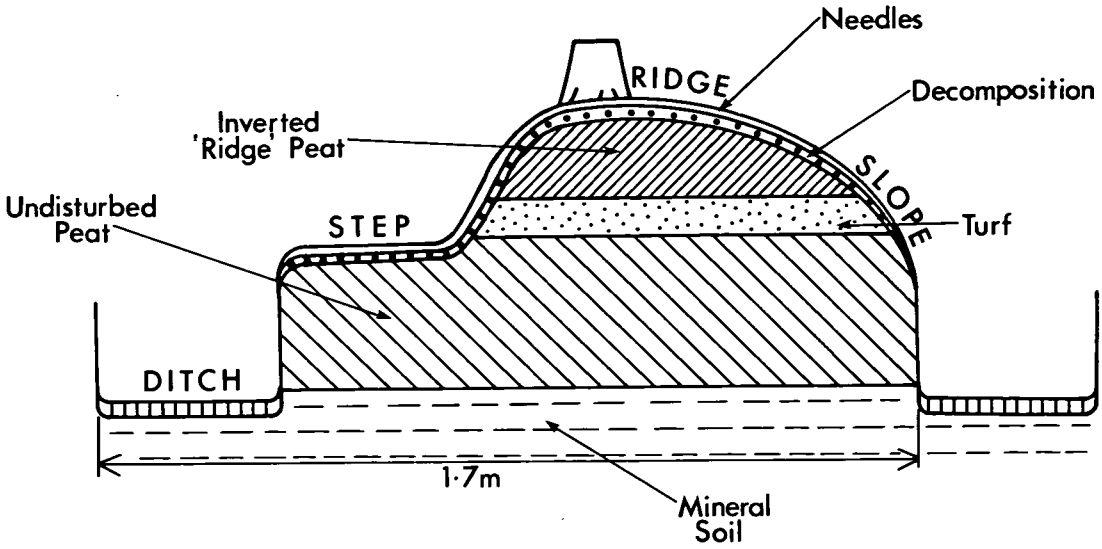
To complement other aspects of a programme concerned with effects of the physical environment on the growth of a young plantation of Sitka spruce, *Picea sitchensis* (Bong.) Car., growing on a peaty gley soil in south Scotland, observations were made of root distribution and growth. Essentially, the provision of water and mineral nutrients is a function of 'fine' roots, whereas the mechanical functions of anchorage and support (for the trunk and canopy) are associated with large coarser roots. To investigate the changing populations and distributions of systems of fine roots, soil cores were taken at weekly intervals, from May until September, using stratified random samples, ensuring that on each occasion 4 cores were removed from the ditch, step, ridge and slope sections of a planting unit at each of 3 locations, (i) within 0.2 m of planting position, (ii) midway between planting positions and (iii) intermediate between (i) and (ii) (Figure 29). To be able to assess the dynamics of fine roots in terms of root lengths per unit volume of soil, a possibly more critical index than estimates of root weight, considerable care was taken when sorting the cores.

1. Occurrence of roots

The detailed study of the spatial distribution of fine roots < 1.0 mm (diameter) shows that (i) most growth occurred from mid-June to late July and (ii) changes in root lengths and weights cm^{-3} of soil were not synchronous, the former usually following the latter. In mid-July, increases in root length were occurring when weights cm^{-3} of soil were decreasing (Figure 30). Concentrations of fine roots were substantially larger in freshly-fallen needles, decomposing ground vegetation and the layer of inverted turf than in undisturbed peat, with roots being absent from many of the samples taken from undisturbed mineral soil. Of the total length of fine roots, 70% was found in horizons at, or above, the original ground level, with 75% of these being confined to ridge sections where concentrations of available mineral elements were maximal. Along rows, fine roots tended to be concentrated close to the trunks of trees, particularly downslope, with fewest per unit volume of soil midway between trees. At right angles to the line of planting, the largest concentrations of fine roots occurred in the ridges and slope sections adjacent to trees, with fewer in the step region and least in the ditches (Figure 29). These patterns of root distribution probably reflect the interplay between differing (i) soil conditions and (ii) distances from the bases of parent trees. Preliminary observations of soil moisture distribution suggest that amounts of rain reaching the forest floor were spatially variable and that rewetting of soil was often restricted to surface horizons during summer. From these and other observations, it was suggested that prolific surface rooting could be attributed to the effects of the relatively abundant supply of mineral elements in surface horizons which became available by mass flow as a result of frequent re-wetting (Ford & Deans, 1977).

On examining the partitioning of rain (precipitation) falling on a forest into stemflow and throughfall, not overlooking the amounts lost by evaporation after being intercepted, it was found that amounts of throughfall reaching the forest floor were largest per unit area near the bases of trees and least near ditches where canopy foliage was densest (Ford & Deans, 1978). Throughfall accounted for 60% of the moisture reaching the forest floor during the summer, stemflow accounting for the remainder and adding to the already relatively large amounts of moisture, attributed to throughfall, near stem bases. Thus, the spatial pattern of fine root distribution mirrors that of moisture, a relation prompting an investigation of the influence of soil moisture on the dynamics of fine roots. Samples were taken from areas (25 x 25 cm) of densely rooted ridge sections, 20-45 cm downslope from the nearest tree. Five cores were extracted to a depth of ε 50 cm on 20 occasions at 5-day intervals from 3 May to 6 August 1976. Using an improved version of a root measuring device described by Rowse and Phillips (1974), it was found that populations of

A/SECTION THROUGH RIDGE (PLANTING UNIT)



B/GROUND PLAN

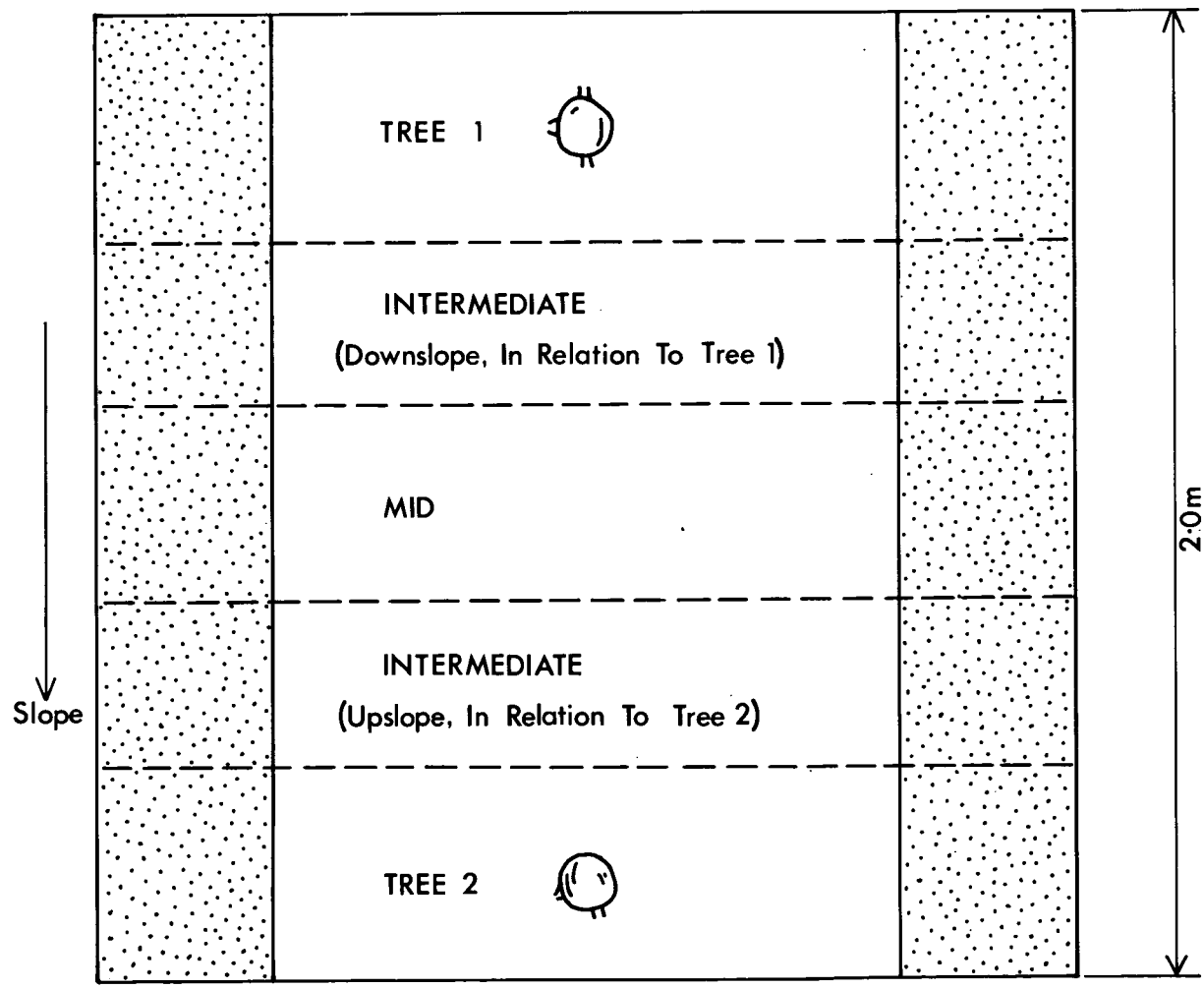


Fig. 29 *Diagrams illustrating A. section through a ridge showing the arrangement of disturbed and undisturbed horizons when planting Sitka spruce and B. ground plan with zones from which stratified-random soil cores were taken at weekly intervals.*

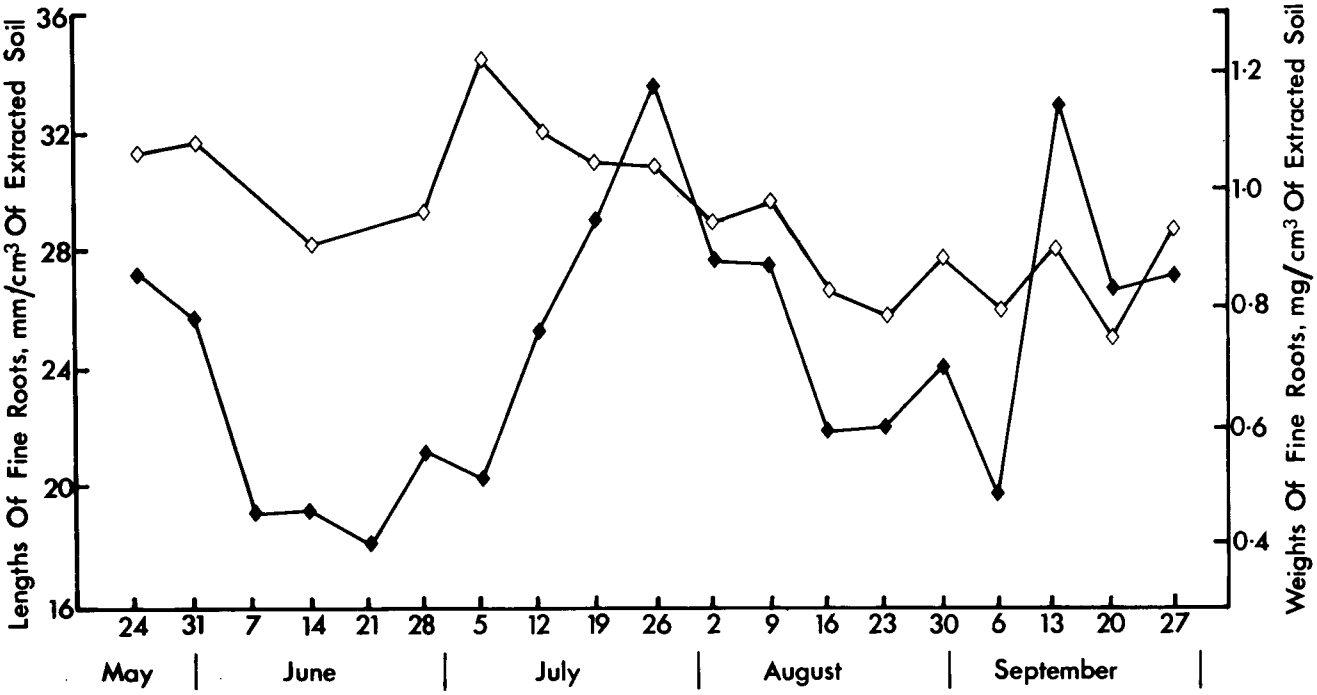


Fig. 30 *Seasonally changing weights (◇) and lengths (◆) of fine roots in a plantation of Sitka spruce, 11 years old. (Roots assessed per cm³ of soil).*

fine roots increased in concert with soil temperatures from May to early June, a period of persistent heavy rainfall when soil moisture tensions were very small (close to saturation) (Figure 31). Thereafter, amounts of roots slightly decreased to a quantity that was sustained until late June, a period including the major phase of shoot extension when roots and shoots were competing for probably limited resources. From late June onwards, root populations were significantly and negatively correlated with soil moisture tensions, suggesting that there was insufficient moisture available to sustain root growth even though soil temperatures were favourable. With other results (Deans, 1979), these data indicate that densely planted forests are capable of transforming moist sites into sites of moisture deficit within 14 years of planting, and in so doing possibly adversely affect the functioning of fine roots which, in drier conditions, may be less able to facilitate the uptake of mineral nutrients. In coming to this tentative conclusion, caution is required because little is known about (i) the distribution and functioning of thick roots relative to that of fine roots, (ii) the effects of differing moisture tensions on nutrient uptake and hence tree performance and (iii) the effects of tree canopies of different sizes and configurations on the partitioning of rainfall.

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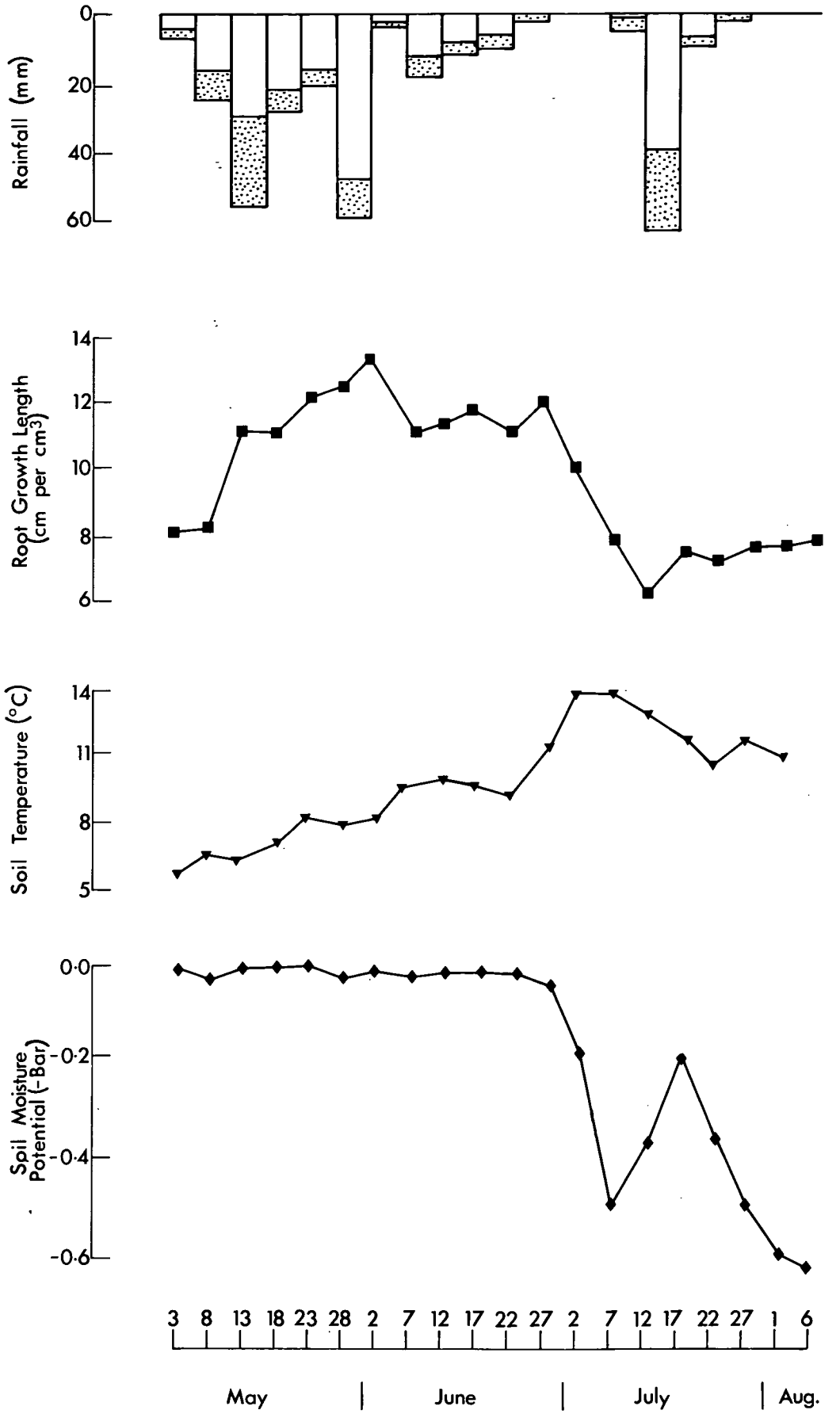

Fig.31 *Relation between the root growth of Sitka spruce, in the inverted turf horizon (see Figure 29), and 2 environmental factors at the same location affecting a plantation 14 years old. The stippled proportions of rainfall indicate rainfall intercepted by, and evaporated from, the canopy.*

Trees and the deposition of atmospheric pollutants

13. DRY DEPOSITION OF AIRBORNE POLLUTANTS ON FORESTS

D. FOWLER

During the last decade, determined efforts have been made to elucidate (i) the factors influencing the removal and fate of atmospheric pollutants, and (ii) their effects on terrestrial and aquatic ecosystems. For the former, methods have ranged from field experiments using SO_2 labelled with the radioisotope ^{35}S (Garland *et al.*, 1973) to laboratory measurements using a mass balance technique (Hill & Chamberlain, 1976), with most information being obtained from micrometeorological methods developed originally for studies of heat and momentum exchange between vegetation and the atmosphere.

Gaseous or particulate material captured directly by the earth's surface from the atmosphere, regardless of the state of the surface or the mechanism operating, is referred to as dry deposition in contrast to wet deposition, the transfer of substances from the atmosphere in aqueous solution (rain) or suspension. All gases and particles smaller than about 10 μm are transported to surfaces by turbulent transfer processes, and, as most atmospheric particles are in this size category, dry deposition tends to be interchangeable with turbulent deposition. In contrast, the relatively small fraction, by mass, of large particles (those with diameters $\geqslant$10 μm) and appreciable terminal velocities are deposited under the influence of gravity.

1. The removal of atmospheric pollutants

1.1 Gases

The rates of dry deposition of gases are determined by 2 largely independent processes, (i) turbulent diffusion which transports gas molecules from the free atmosphere to a surface (in reality, surfaces have viscous boundary layers of air through which gases must be transported by molecular diffusion), and (ii) the affinity (chemical or physical) of the absorbing surface for the gas in question.

Crop canopies have at least 3 different sites at which gas molecules may be absorbed, (i) plant cuticles, (ii) the lining of sub-stomatal cavities and (iii) the soil surface. Each of these has a different affinity for different gases, each varying independently of the other. Surface water, whether rain or dew, acts as an additional 'sink' and further complicates the picture.

Of a wide range of methods available for measuring deposition rates, micrometeorological techniques have helped most in defining mechanisms. They average over a large area of surface, are non-destructive and enable fluxes to be obtained over short periods (~20 minutes) during which surface and atmospheric conditions are generally reasonably constant. Although they are confined to the atmosphere, micrometeorological measurements enable the influence of atmospheric transfer on rates of deposition to be separated from that of surface affinity. For this, it is convenient to use a resistance analogue described in detail by Thom (1975) and subsequently used for interpreting flux measurements made of pollutant gases by, among others, Garland (1978) and Fowler (1978).

The vertical flux of pollutant gas, Fp, to suitable surfaces (extensive level areas of uniform vegetation) is proportional to $\partial\chi/\partial z$, the vertical concentration gradient of pollutant gas in the turbulent boundary layer over these surfaces:

$$Fp = -Kp \frac{\partial \chi}{\partial z} \qquad (1)$$

where Kp, the constant of proportionality, is the eddy diffusivity for the gas in question.

Integrating (1) with respect to height between Z_1 and Z_2:

$$Fp = \chi p\,(Z_2) - \chi p\,(Z_1) \qquad (2)$$

$$\int_{Z_1}^{Z_2} \frac{\partial Z}{Kp}$$

—a relationship analogous to Ohm's law. Assuming that the surface concentration is zero, and that the lower limit of the integral is the surface, then equation (2) may be simplified:

$$r_t(Z_2) = \frac{\chi(Z_2)}{Fp}$$

The flux and hence total resistance, r_t, may be obtained from measurements of vertical gradients, above suitable surfaces, of (i) wind-speed, (ii) air temperature and (iii) concentrations of pollutant gas.

The total resistance to pollutant gas deposition is the sum of atmospheric, r_a and r_b, and surface r_c components (Figure 32). Atmospheric terms r_a and r_b may be estimated directly from wind speed and air temperature profiles, and thus the surface components, r_{c1}, r_{c2} and r_{c3}, may be estimated as a single residual term, r_c. If measurements of $r(a + b)$ equal r_t, then the surface is behaving as a perfect sink and is absorbing the gas as quickly as the eddy diffusion processes can supply it. However, when a residual term exists (r_c), the surface or canopy resistance, we have a measure of the affinity of the absorbing surface (all sinks acting in parallel) for the gas in question.

This background provides a framework to interrelate measurements being made of fluxes of SO_2 at ITE's experimental forest site, kindly made available by the Forestry Commission, in Ochil Forest. The main sinks for SO_2 in a forest canopy will be measured, and, from them, the different parts of the resistance network (Figure 32) will be evaluated, enabling the prediction of rates of deposition on forests to be made in a wide range of surface and atmospheric conditions.

From a compilation of published deposition rates, Garland (1978) showed that canopy resistance to SO_2 deposition increased with vegetation height. Canopy resistance to water vapour transfer also increases with vegetation height, an adaptation towards stricter control of water loss in tall vegetation. It seems probable, therefore, that stomata, the major source of water vapour in vegetation, are important sites of SO_2 uptake in tall vegetation, just as they are in short vegetation (Fowler, 1978). Aerodynamic resistance for mass transfer to and from vegetation decreases with increasing vegetation height, so that canopy resistance to SO_2 transfer increases as a proportion of total resistance as vegetation height increases.

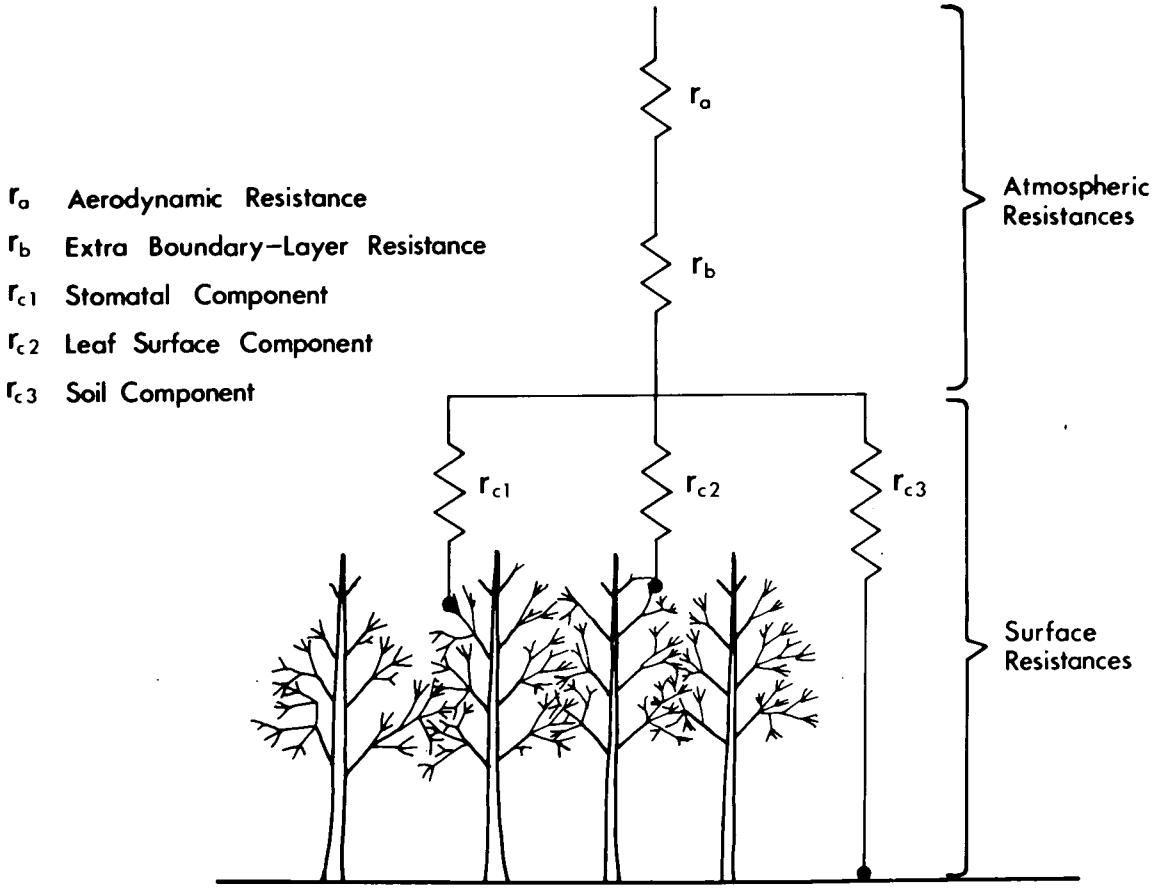

Fig. 32 *Resistances to pollutant gas deposition in forest canopies.*

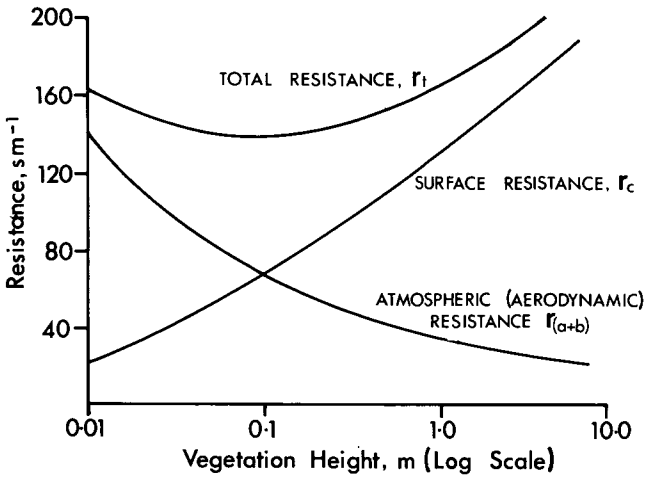

Fig. 33 *Relation between vegetation height and mean surface (r_c) and atmospheric (r_a + r_b) resistances to SO_2 deposition.*

The changes with vegetation height of aerodynamic and canopy resistance to SO_2 transfer are such that overall resistance to transfer remains approximately constant over a large height range (Figure 33). Extrapolation in this figure to the height range appropriate for forests is fairly speculative, but, if correct, it shows that surface conditions effectively control rates of SO_2 deposition. Stomatal movements and chemical and physical reactions between leaf surfaces and SO_2 are therefore likely to be the major factors influencing forest deposition rates. In the presence of surface moisture, surface resistances would be small and the large rates of deposition would be set by atmospheric resistances, provided that the pH of surface water film exceeds 4.0. Because the solubility of SO_2 declines with increasing acidity, surface resistance would eventually reappear as an important factor if surface moisture films were to become more acid than pH 4, as a result of the absorption and oxidation of SO_2 molecules. The point at which surface resistance becomes dominant lies in the range pH 3.0 to 3.5.

1.2 Particles

Turbulent diffusion processes are responsible for the transport of particles from the free atmosphere to the viscous boundary layer close to surfaces, but transport of particles through this sub-layer (distances of the order of 1mm) and subsequent capture differ considerably from that of gases. The large particles (diameter $>$ 1μm) are transported through the sub-layer by their own inertia and by gravitational forces, whereas particles appreciably smaller than 0.1 μm are transported by Brownian diffusion. In between, in the size range of 0.1 to 1 μm, particles do not have an effective 'vehicle' for transfer through this boundary layer and consequently their deposition rates are minimal (Chamberlain, 1975). Most sulphur-containing particles are in the size range 0.1 - 1.0 μm and, inevitably, deposition velocities are small. This low velocity, linked with the generally small ambient concentrations of sulphur particles, 2 to 8 $\mu g\ S\ m^{-3}$, makes the measurement of their fluxes in a forest very difficult, although there is now a prospect of success using an eddy correlation technique.

2. Effects of atmospheric pollutants

Most primary air pollutants SO_2, O_3 NO_x and HF are reactive gases. It would not be surprising if they and/or their secondary and tertiary reaction products were to react with the protective layers of conifer needles. Using an arbitrary system of assessment, it was found that the structure of surface configurations of epicuticular waxes was lost sooner by needles of Scots pine *(Pinus sylvestris)* growing at a polluted site in south Yorkshire than at a clean air site in the Lammermuir hills of south-east Scotland (Figure 34), care having been taken to ensure that both stands of trees were grown from seeds of the same provenance. The differences in wax structure of needles, which survive for 3 years, were greatest in the period 3 to 9 months after needle expansion.

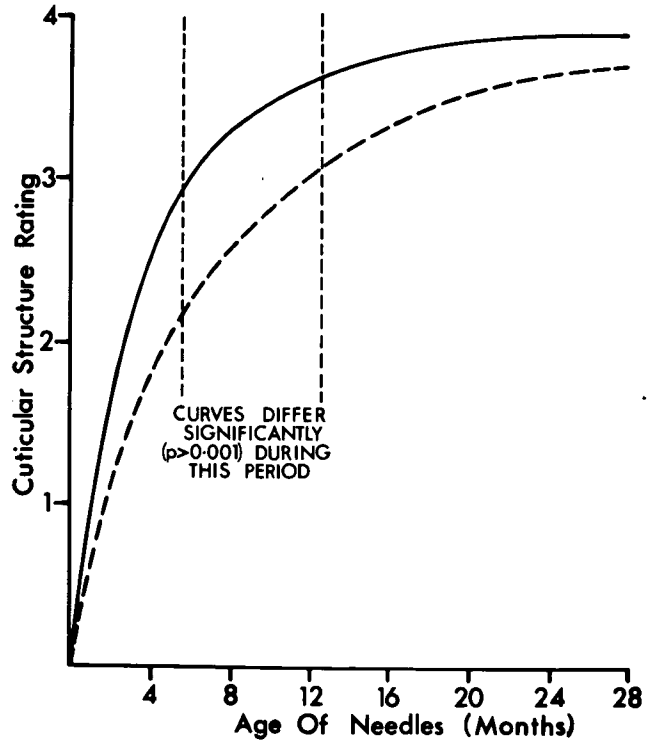

Fig. 34 *Changes in the structure of epicuticular waxes of ageing needles of Scots pine grown at sites with either sulphur polluted (—) or clean (——) ambient air. CSR = CUTICLE STRUCTURE RATING, 0 and 4 being the least, and most, eroded, respectively.*

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14. WET DEPOSITION AND THE MOVEMENT OF POLLUTANTS THROUGH FORESTS

I.A. NICHOLSON

With a greater or lesser degree of certainty, it has been suggested that sulphur dioxide and other sulphur-derived pollutants can directly and indirectly affect the productivity of terrestrial and aquatic ecosystems. Although SO_2 and acid precipitation, resulting from the hydration and oxidation of SO_2, may separately affect the different ecosystems, it is often difficult to distinguish their influences one from the other, or from the combined effects of mixtures including other types of pollutant, eg NO_X and ozone. Our knowledge is still surprisingly deficient.

Research within ITE is concentrated on the fate and effects of sulphur pollutants, measured above and within a stand of Scots pine *(Pinus sylvestris)* in the Devilla section of the Forestry Commission's Ochil forest in central Scotland. Observations are being made of dry deposition, the direct transfer of gaseous and particulate material from the atmosphere to surfaces, and wet deposition, the transfer of an element or substance from the atmosphere in aqueous solution or suspension, whether rain, snow or fog, wet deposition being the subject of this chapter.

1. Wet deposition and precipitation acidity

1.1 Wet deposition

At distances from emission sources, amounts of atmospheric SO_2 are depleted as a result of (i) its dry deposition and (ii) its oxidation to sulphate, SO_4^{2-}/SO_2 ratios tending to increase with distances from sources.

Sulphur dioxide is absorbed by water droplets in the cloud-producing layers, but, although it is very soluble, solubility is nevertheless strongly pH-dependent, the amounts absorbed decreasing as the pH of water droplets decreases. This removal of SO_2 is known as rainout, whereas the collection (scavenging) of gaseous and particulate sulphur by falling raindrops is known as washout. Small drops are more efficient scavengers than large drops and therefore remove more SO_2 per mm of precipitation.

Raindrops, drizzle and other relatively large drops > 0.5 mm are deposited by sedimentation. In contrast, the much smaller fog droplets ($< 100\ \mu$, characteristically $10\ \mu$) reach surfaces by physical processes similar to those responsible for dry deposition of small particles (turbulent impaction); their deposition is therefore significantly affected by the nature of the different surfaces, eg the size and distribution of leaves.

1.2 Changing precipitation chemistry

The formation of sulphuric acid is mainly responsible for acidifying precipitation. Rain samples from North America, for example, showed that sulphate accounted for *c* 62% of the anions present (Likens & Bormann, 1974). Major changes in precipitation acidity, similarly largely attributable to the presence of sulphate, have been recorded in western and northern Europe including Norway and Sweden, where amounts of deposited sulphate, of non-marine origin, increased appreciably between 1955 and 1970 (Malmer, 1974): in Britain, Martin (1978) concluded from a limited amount of data that the largest increase in rain acidity occurred before 1957.

Although Gorham (1957) presented evidence, as far back as the mid-1950s, suggesting that industrial pollution was increasing the acidity of rain in the English Lake District, his observations had surprisingly little impact, at that time, on ecological research. Evidence of increasing acidity and its effects in Scandinavia was first documented in a Swedish government report in 1967.

To add to the analysis made of rain collected at a few locations scattered over the length of Britain, ITE established, in 1977, a relatively intensive network covering much of northern Britain. Compared with the very polluted areas in southern Norway, most sites in Britain appear to receive proportionately less rain of low pH, and the sulphate content of rain is less (Figure 35); nonetheless rain in northern Britain is usually considerably more acid than pH 5.7 (the so-called "neutral" point for rain) and on some occasions, at some stations, very acid rain containing large concentrations of sulphur have been recorded.

2. Effects of forests on wet deposition

Setting aside the possibility that forests on a regional scale may influence the occurrence of precipitation, their structures also (i) alter the ways in which incident precipitation is partitioned into stemflow, throughfall and interception and (ii) affect the deposition of fog.

2.1 Deposition of rain and snow within forests

Most forests, natural and man-made, are structured with dominant, sub-dominant and suppressed trees, shrub and ground floras which act as a

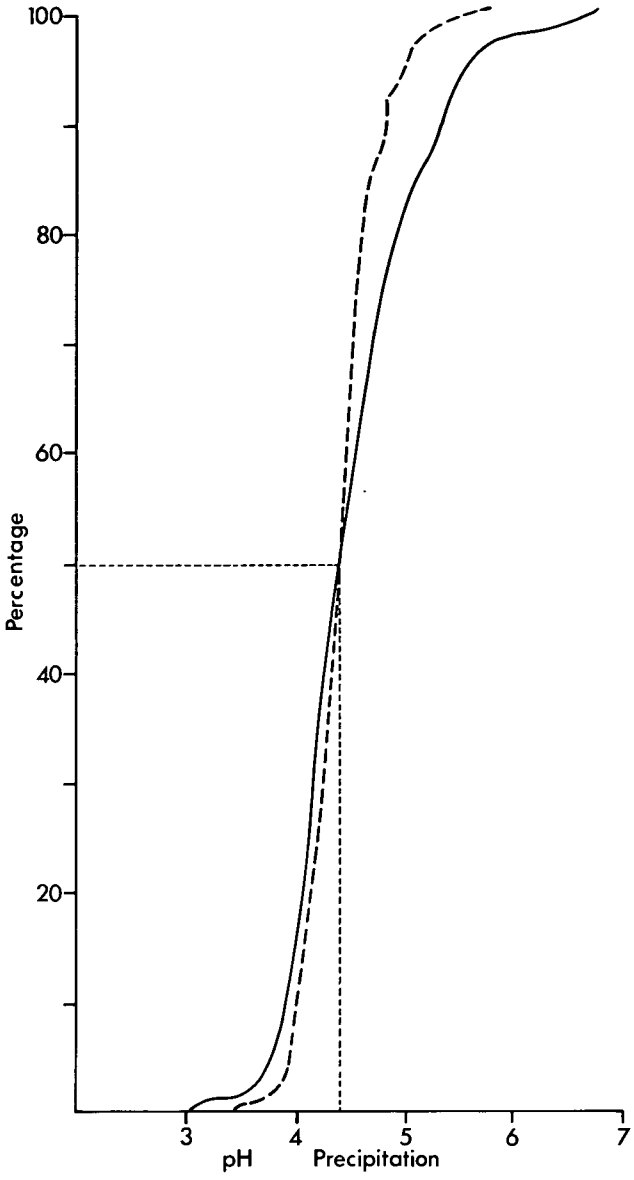

Fig. 35 *Cumulative distributions showing percentage of total precipitation with pH lower than given values. 1978/79 means for Banchory (—) are compared with those for 1972/75 at Birkenes, Norway (——) (Dovland* et al., *1976). Mean annual precipitation at Banchory and Birkenes amounted to 780 and 3,900 mm respectively.*

series of 'baffles' ensuring that very little precipitation falls directly on to soil. Passage through forests will be influenced by the density of each layer of the canopy, with amounts of wet deposition being greater on some layers, or parts of layers, than on others. Snow penetrates vegetation less readily than rainfall and therefore amounts deposited tend to be spatially disparate, usually with large accumulations, attributable to drifting, in clearings and at the forest edge.

2.2 Fog deposition

Whereas fog blown inland from the sea sometimes contains appreciable quantities of solutes (Azevedo & Morgan, 1974), inversion fogs in polluted atmospheres tend to have large concentrations of pollutants. Fog deposition from advection fogs, which are caused by cooling resulting from advection of warmer air over a colder surface, has been studied in coastal areas of Japan and on the Pacific coast of North America where such fogs are commonplace. It has been found that 6 - 10 times as much fog drip was trapped by forests as was collected on the ground in nearby open fields, this filtering effect being attributed to the transport of fog particles to foliage and branches by turbulent diffusion. Additionally, large quantities of precipitation have been recorded at the edges of the forests where fog was driven by strong winds, so-called horizontal deposition. (Imahori, 1953; Oura, 1953 *a, b*; Yosida, 1953).

In foggy conditions, plant surfaces are moist. These moisture films are important because they:

(i) provide an efficient sink for gaseous atmospheric pollutants (Fowler, 1978; Brimblecombe, 1978);

(ii) possibly enhance leaf leaching;

and (iii) increase the possibilities of interactions between pollutants occurring by wet and dry deposition.

3. Precipitation input: 'pathways' and changes in chemical composition

3.1 Effects of foliage on precipitation chemistry

'Sulphur' can be deposited on the surfaces of leaves and bark and absorbed in the gas phase through leaf stomata when it may be metabolised without necessarily causing damage. Many studies have shown that the composition of rainwater changes as it passes over plant surfaces and that different tree species have different effects on throughfall (eg Madgwick & Ovington, 1959; Henderson *et al.*, 1977) and stemflow, the largest concentrations of solutes and suspended matter usually being found in this fraction (Voigt, 1960; Abrahamsen *et al.*, 1975). Bjor and his colleagues (1974) working in Norway found that throughfall beneath Norway spruce and Scots pine was more acid and contained larger concentrations of sulphate than precipitation collected in open terrain, whereas that of birch contained smaller amounts of strong acid (Table 17).

The composition of water draining from leaves and stems is usually augmented by the addition of surface deposits and foliar leachates and depleted by the removal of substances, including moisture, by leaf absorption.

TABLE 17 Relative effects of canopies of different tree species on amounts and chemical composition of throughfall, comparisons being made with precipitation collected on nearby open terrain whose amounts, and composition, were taken as 100 (Bjor *et al.*, 1974).

Species of tree	Position of rain gauges+	Volume of throughfall as % of incident precipitation†	Relative concentrations of different chemical constituents		
			Strong Acid	Mg^{2+}	SO_4^{2-}
Norway spruce	Inner	35	138	102	131
	Outer	99	181	187	211
Scots pine	Inner	82	297	259	215
	Outer	83	248	230	202
Birch	Inner	92	92	158	101
	Outer	71	62	161	89
Open terrain		100	100	100	100

+ Positions relative to canopy—inner, near trunk; outer, at perimeter.

† The deficits in relation to open terrain are attributed to 'interception' losses and amounts of stemflow which were not measured.

TABLE 18 Data illustrating effects of antecedent weather on amounts of sulphate-sulphur removed from surfaces by washing leaves of holly, and bark of ash, birch and holly taken from trees growing around Manchester. Data from Parr's Fold, a site known to have received prolonged heavy rain (>30 mm in 24 h) immediately before sampling in December, are compared with data from 5 other sites (in the same 'zone' of atmospheric pollution: winter mean conc. >150 $\mu g\ SO_2\ m^{-3}$) sampled subsequently during the same winter. Values are also shown for samples taken from the same sites sampled in summer after a long period without rainfall (Kinnaird *et al.*, Unpubl.).

	Leaves (Holly)			Bark (Means of ash, birch, and holly)		
	Parr's Fold (a)	Other sites (b)	a/b (%)	Parr's Fold (c)	Other sites (d)	c/d (%)
	Amounts of SO_4 - S mg m^{-2}					
I The sample at Parr's Fold, unlike those at other sites, was taken immediately after prolonged heavy rain: observations made in winter	0.1	1.1	9	<0.2	1.9	<10
II The sample at Parr's Fold, like those at other sites, was taken after a prolonged dry spell: observations made in summer	1.6	3.1	52	2.4	5.7	42

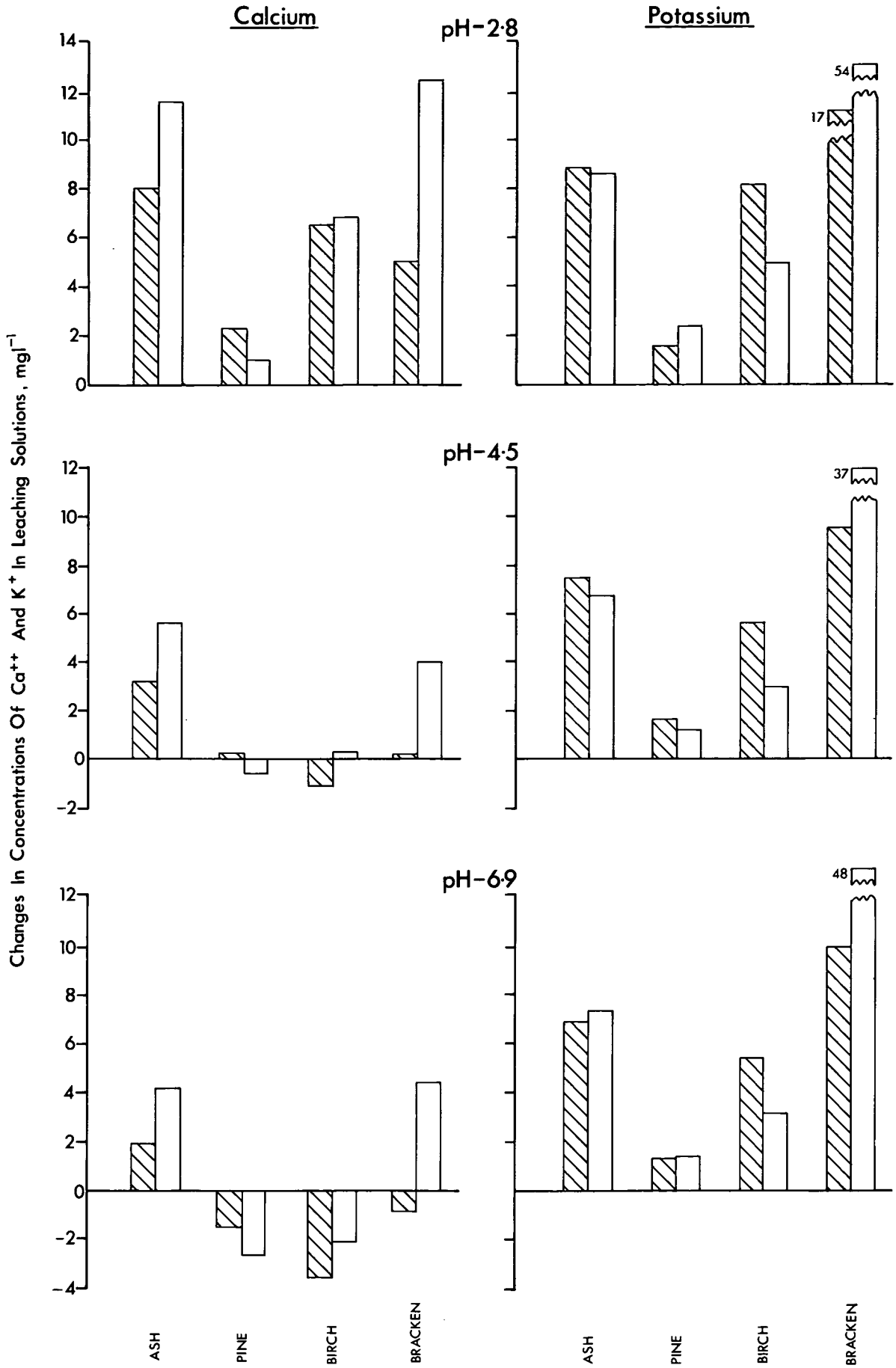

Fig. 36 *Effects of increasing the acidity of leaching solutions from pH 6.9 to 2.8 on the release of Ca++ and K+ from detached leaves of ash, Scots pine, birch and bracken. Experiments done in August* ▨ *and October* □ .

Surface deposits

In and around urban areas, bark and leaves of deciduous and evergreen species accumulate, on their surfaces, relatively large amounts of sulphate which can be readily depleted by rain. (Table 18).

Leachates

It has been known for a long time that amounts of leachates are affected by internal and external factors but the effect of strongly acid rain, which increases cation leaching, was only recently reported (Wood & Bormann, 1975). Experiments done with detached leaves of ash, Scots pine, birch and bracken have shown that increasing amounts of Ca^{2+} were leached when washed with increasingly acidic simulated rain, the effect on K^+ leaching being much less marked (Kinnaird & Nicholson, unpubl.) (Figure 36).

Substances absorbed

Whereas surface deposits and leachates may augment the concentrations of solutes and suspended matter in throughfall and stemflow, some solutes and water may be lost by absorption (Voigt & Swolinski, 1964). Many substances can be absorbed (Tukey *et al.*, 1956; Franke, 1967) including nitrate and ammonium ions by foliage of Norway spruce, Scots pine and birch (Abrahamsen *et al.*, 1976); foliage of Norway spruce was found to absorb phosphorus and potassium (Kilian, 1977). Even in the dormant season, the bark of fruit trees has been found to accumulate phosphorus and potassium by absorption.

3.2 Woodland structure and re-distribution of precipitation

In forests with many tree species providing a complex series of "baffles", the route by which precipitation reaches the ground is likely to be more complex than in a single-species plantation forest, as exists at the ITE study area in Devilla forest. Here precipitation may reach the soil (i) after passage through the canopy without contact with any plant parts (representing true wet deposition to the soil), (ii) by dripping from the foliage or (iii) by stemflow. Of these 'pathways' stemflow is of special interest. The absolute amounts of water involved may be relatively unimportant when considering the water budget of the forest system, for example stemflow may only account for 1-5% of the total precipitation (Zinke, 1967); but the input of water and dissolved substances to the soil is disproportionately large when calculated as a depth of water falling on a surface equal to the ground area occupied by the tree stem. In some studies, amounts of water reaching the soil in these localised areas have been many times the amounts deposited on equivalent areas elsewhere in a forest (Reynolds & Leyton, 1963).

Interestingly, the large amounts of sulphate found on the bark of pine in urban areas of the UK are paralleled by results from southern Norway where stemflow from Scots pine, compared with that of Norway spruce and birch, contained particularly large concentrations of sulphate. With some exceptions (eg Zinke, 1962; Adriano & Pinder, 1977), few studies, since the early work of Müller (1887), have considered the ways in which soil properties beneath forest canopies are patterned. But does the addition of pollutants increase the podsolizing effects of stemflow noted by Mina (1967)?

4. Development of research on wet deposition

At the risk of giving a distorted picture (by omitting problems of dry deposition), 2 areas of research need particular attention: (i) the atmosphere/leaf surface interface where reactions occur that may influence the deposition and transformation of substances which interfere with exchange reactions, internal and external, with photosynthesis, transpiration and other leaf functions and with leaf surface microbes, and (ii) the impact of stemflow on soil processes and properties.

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15. AN IMPROVED METHOD OF ESTIMATING THE CONTRIBUTION OF CROWN LEACHATES TO THE CHEMICAL COMPOSITION OF RAIN COLLECTED BENEATH TREES

K.H. LAKHANI

Amounts of solutes and suspended matter in rainwater collected as stemflow and throughfall beneath trees are generally greater than those in rainwater collected in the open. This enrichment, as rainwater passes over foliage and branches, is partly attributable to the removal of substances previously deposited on foliage and branches by impaction or adsorption, and partly to substances leached from within plants (ie crown leaching). The former provides a new input to the system, whereas crown leaching facilitates recycling. But how can the contributions made by these 2 processes be separately identified?

Atmospheric inputs can be estimated directly and indirectly. They can be estimated directly from (i) catches of airborne particles (White & Turner, 1970), but problems arise when ascribing amounts to unit areas of forest, and (ii) with methods based on nutrient budgets (Likens *et al.*, 1977) which tend to lack sensitivity because the fluxes of different substances are usually small relative to the sizes of the 'sinks', particularly soil. Indirect methods have relied on comparisons made of the chemical composition of stemflow and throughfall with those of rainfall collected in the open during the same period of time. However, the compositions of stemflow and throughfall reflect the extent of crown leaching in addition to dry deposition and wet deposition, whereas those of rainfall collected in gauges in the open reflect the latter, plus a small fraction of dry deposition (accumulated since the gauge was cleaned). Mayer and Ulrich (1974) argued that crown leaching of deciduous trees could be assumed to be negligible during leafless winter months, and then proceeded to obtain estimates of dry deposition during winter. Their method, however, assumes that significant leaching occurs only through leaves, and that rates of dry deposition to leafless trees in winter are similar to those to leafy trees during summer months. Miller *et al.* (1976), working with Corsican pine, *Pinus nigra var. maritima* (Ait.) Melv., observed that amounts of solutes and suspended matter in stemflow and throughfall (kg ha^{-1} wk^{-1}) were linearly and directly related to their amounts in rainfall collected in the open. They used the intercept of this regression as a measure of crown leaching, assuming that inputs in rain and from the removal of surface deposits could be combined as a single variable. However, the validity of this assumption has recently been questioned by Lakhani and Miller (1980) who were concerned with the partitioning of rain in a plantation of Corsican pine. Dr H.G. Miller of the Macaulay Institute analysed the chemical composition of:

(i) stemflow and throughfall

(ii) rain collected in the open in Nipher-shielded rain gauges (open gauges)

and (iii) rain collected in the open in funnels surmounted by an inert wind-filter of polyethylene coated wire mesh (filter gauges).

Samples of (i), (ii) and (iii) were taken simultaneously and at equally spaced intervals during the course of 2 years, the inclusion of filter gauges being essential if amounts of crown leaching were to be separately identified from those of wet and dry deposition.

1. Method

Suppose that rainwater is collected during 'n' equal time periods. Let the weight (kg ha^{-1}) of a given substance in stemflow and throughfall during the 'i'th time period be X_{1i}; and, let the corresponding weights of that substance in open and filter gauges be X_{2i} and X_{3i} respectively. Thus, the field data will consist of n triplets of observations X_{1i}, X_{2i}, X_{3i} (i = 1, 2, ..., n). If the wet deposition, dry deposition and leaching of different substances (kg ha^{-1}) during the 'i'th time period are denoted W_i, D_i and L_i, then the X_{ji} values (j = 1, 2, 3; i = 1, 2, ..., n) can be expressed in terms of these components and other effects. X_1, the concentration of different substances in combined stemflow and throughfall, is essentially the total of wet deposition, dry deposition and leaching during the 'i'th time period. But some part of some substances will be 'lost' through (i) foliar absorption, f_i, and (ii) the incomplete removal of surface deposits whatever their origin, l_i. On the other hand, there will be some gain, g_i, because rain of the 'i'th time interval will succeed in removing some of the surface deposits remaining from earlier periods. Additionally, X_1, the composition of stemflow and throughfall, will be subject to chance variations represented by the error term, e_i. Thus,

$$X_{1i} = W_i + D_i + L_i - f_i - l_i + g_i + e_i \qquad (1)$$

The loss and gain terms, l_i and g_i, are unknown functions of a range of variables which tend to cancel each other. By absorbing them and the unknown foliar absorption term, f_i, a new error term e'_i is evolved:

$e_{1i} = e_i - f_i - I_i + g_i$.

Thus $X_{1i} = W_i + D_i + L_i + e_{1i}$ (2)

Because the chemical composition of rain collected in the open gauge, X_{2i}, will be mainly attributed to wet deposition, with some contamination from dry deposition which is assumed to be proportional to dry deposition on forests,

$$X_{2i} = W_i + aD_i + e2i \quad (3)$$

where 'a' is a positive constant of proportionality and 'e_{2i}' is a random error term.

Finally, the chemical constituents in the filter gauge, X_{3i}, will also be attributable to wet deposition and dry deposition. Because their wind-filters will intercept some of the non-vertical rainfall which would otherwise not be captured, the filter gauges will tend to collect greater volumes of rain than open gauges. If the rain collection efficiency of filter gauges, relative to that of open gauges, is assumed to be constant, and if most wet deposition is attributable to rain in contrast to fog and mist, then amounts of wet deposition in X_{3i} can be equated to 'kW_i' where 'k' is an unknown positive constant. If it is assumed that filter gauges, as regards dry deposition, have a catching efficiency of 'b' relative to the catching efficiency of forests, then:

$$X_{3i} = kW_i + bD_i + e_{3i} \quad (4)$$

where e_{3i} is a random error term. As k is likely to be greater than 1, and b greater than a, X_{3i} will be expected to be greater than X_{2i}.

If V_i and U_i are the volumes of liquid collected in the open, and in filter gauges, during the 'i'th time period, then the estimate (k) of the constant k is given by:

$$k = \Sigma U_i / \Sigma V_i.$$

Dividing (4) by k gives the adjusted observation:

$$X'_{3i} = X_{3i}/k = W_i + b'D_i + e'_{3i} \quad (5)$$

where $b' = b/k$, $e'_{3i} = e_{3i}/k$ and $k/k = 1$.

To eliminate the wet deposition term W_i from equations (2), (3) and (5), X_{2i} is subtracted from X_{1i} and X'_{3i} respectively to obtain the derived variables:

$$Y_i = X_{1i} - X_{2i} = (1 - a)D_i + L_i + e_{1i} - e_{2i} \quad (6)$$

and $$X_i = X'_{3i} - X_{2i} = (b' - a)D_i + e'_{3i} - e_{2i} \quad (7)$$

Thus, if L_i is independent of D_i, with the mean of L_i equal to M_L (this condition is less strict than the special case that L_i be constant), then Y_i is linearly related to X_i with the slope equal to $(1 - a)/(b' - a)$ and the intercept equal to M_L. Problems of estimating the parameters defining the structural relationship between 2 variables (in this instance X_i and Y_i), both of which are subject to random errors, are intrinsically difficult (Kendall & Stuart, 1961). In the present instance, the problems are exacerbated because the error term, e_{2i}, present in both equations, reduces the degree of independence. However, unlike the error terms e_{2i} and e_{3i}, the error term e_{1i} is a conglomeration in which, because of the large spatial variation beneath a forest canopy, even the single term e_i is likely to be large relative to e_{2i} or e_{3i}. On the other hand, because k is likely to be greater than 1, e'_{3i} will tend to be less than e_{3i}. Thus, if it is assumed that e_{1i} is likely to be relatively large compared with e_{2i} or e'_{3i}, then the parameters defining the relationship between Y_i and X_i can be readily estimated using standard regression techniques. Theoretically, the magnitude of the different errors can be controlled by varying the intensity of sampling.

2. Discussion

Previously, Miller *et al.* (1976) used the intercept of the regression of X_{1i} on X_{2i} as an estimate of crown leaching. But, because $X_{1i} \sim W_i + D_i + L_i$ and $X_{2i} \sim W_i + aD_i$, it was necessary to assume that D_i was proportional to W_i, so that they could be treated as a single variable; and also that L_i was independent of W_i. In practice, D_i and W_i are likely to be correlated, but not proportionately. In contrast, L_i and W_i are unlikely to be independent (Abrahamsen *et al.*, 1976).

By including the additional variable, X_{3i}, it has been possible to eliminate W_i from equations (2), (3) and (5) so enabling the estimation of leaching (L_i) on the assumption that they are independent of dry deposition (D_i). In the event, the filter gauge is likely to oversample rainfall, so requiring the adjustment of the X_{3i} values via the estimate of k (see equations (4) and (5)). Alternatively, the gauge may be modified to have a large funnel with inset filter.

In addition to facilitating estimates of crown leaching, the method described in this chapter can be used to estimate dry deposition (D). From equation (7), $X \sim (b' - a)\,D$ and hence $D \sim X/(b' - a)$ which may be written as:

$$(1 - a)D \sim X.\ (1 - a)/(b' - a)$$

with $(1 - a)/(b' - a)$ being estimated from the slope of the regression of Y_i on X_i. The term (X. slope) underestimates mean dry deposition, the extent of the underestimation being equal to a.D, which

tends to zero as 'a' tends to 0, as happens when the open gauge is designed to collect negligible dry deposition.

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Trees and their nutrition and effects on soils

16. GROWTH OF SYCAMORE AND BIRCH IN RELATION TO SOIL CHEMICAL PROPERTIES

A.F. HARRISON and D.R. HELLIWELL

Six seed-lots of sycamore (*Acer pseudoplatanus* L.) and 4 seed-lots of birch (*Betula pendula* Roth.) from various European provenances were grown in a range of Cumbrian soils, in a pot experiment to study variation in seedling response to soil chemical properties. Seedlings from all seed-lots of both species responded in a similar manner to the whole range of soils (Helliwell & Harrison, 1978), so only the relationships between species and soil chemical properties of the soils are examined.

The seed-lots of sycamore were stratified in moist sand at 2°C for 6 weeks before being sown directly and those of birch were germinated on peat to the '2 leaf' stage, before being planted out into the experimental soils in May 1974. Twenty-five soils with a wide range of physical and chemical properties (Table 19) were collected within 40 km of Merlewood. Before filling polythene pots of 2 sizes, each soil was sieved at field moisture through a 13 mm mesh and afterwards thoroughly mixed. After planting, the pots were arranged in a randomized block design on raised gravel beds within a bird and mammal proof cage for protection (Helliwell & Harrison, 1978). They were watered after rain-free days in spring and summer and were periodically weeded before being harvested after 16 months in September 1975. Both tops and roots were dried and weighed. Soil samples for chemical analyses were taken from pots in June/July of the first season, when plants were growing at their fastest rate.

Probably because of an initial advantage attributable to the nutrient content of larger seeds, sycamore grew more than birch. There was an overall correlation (r = 0.75) between the growth of the 2 species, but sycamore grew significantly better than birch on some soils and *vice versa* (Figure 37). There was, however, no significant difference between the growth of different seed-lots within either species (Helliwell & Harrison, 1978). Also, growth of plants in small pots was highly correlated (r = 0.97) with growth of plants in big pots for both species (Table 20).

TABLE 19 Some properties* of 25 Cumbrian soils on which different seed-lots of sycamore and birch were grown

Soil property	min	mean	max
Loss-on-ignition %	7.5	25	89
pH	3.2	4.5	7.9
Total P μgg^{-1}	100	1080	3600
Total N %	0.21	0.82	2.32
Extractable P μgg^{-1} (a)	2.6	12.3	97
Isotopically exchangeable P μgg^{-1} (b)	9.8	191	1700
Phosphatase activity (c)	71	608	3309
Extractable NH_4 -Nμgg^{-1} (d)	4.3	72	220
Extractable NO_3 -Nμgg^{-1} (d)	1	24	61
Extractable K μgg^{-1} (a)	38	129	300
Extractable Ca mg100g^{-1} (a)	10	317	5400
Extractable Fe μgg^{-1} (e)	7	207	1066

(a) Extractable in 2.5% acetic acid (Allen *et. al.*, 1974)

(b) Method 3, (18 hrs), (Harrison, 1975)

(c) Expressed as phenol liberated from disodium phenyl-phosphate at soil pH and 13°C in $\mu gPhg^{-1}$ soil (Harrison, 1979)

(d) Extractable in 15% aqueous KCl

(e) Extractable in ammonium citrate (0.001 M) – HCl (0.02 M) adjusted to soil pH.

*Properties of individual soils have been presented elsewhere (Jeffers, 1977; Helliwell & Harrison, 1978).

TABLE 20 Growth of sycamore and birch seedlings in 25 Cumbrian soils

	Mean dry wt per plant after 16 months' growth (g)		
	Minimum	Mean*	Maximum
Sycamore			
small pots	0.002	3.90	10.44
large pots	0.006	5.76	20.32
Birch			
small pots	0.014	2.38	10.16
large pots	0.014	3.90	19.22

* Means of all replicate seedlings, ie amalgamating all seed-lots

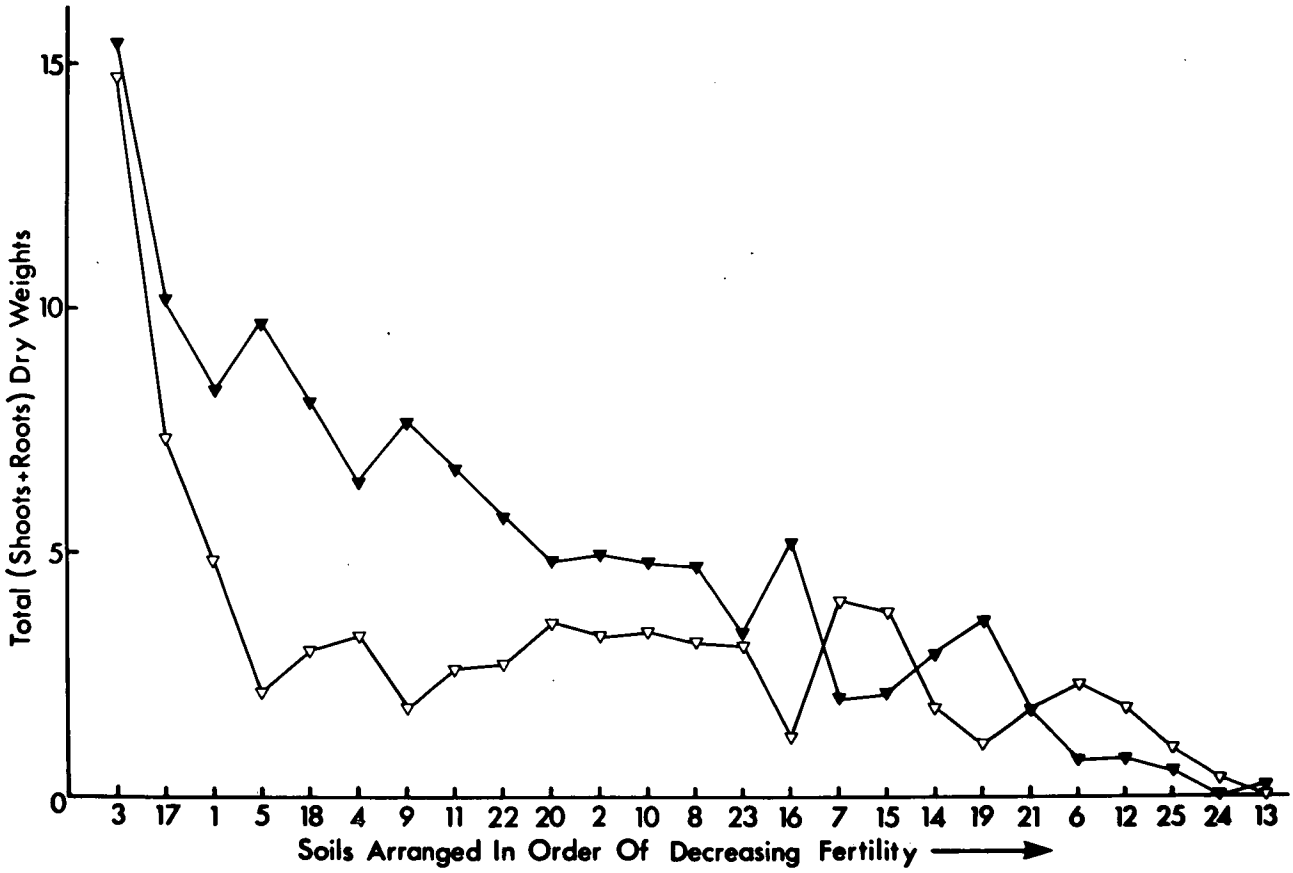


Fig. 37 *Total dry weights of sycamore and silver birch after growing for 16 months in a range of 25 Cumbrian soils. (▼—▼ sycamore, ▽ — ▽ birch).*

Growth in the different soils varied by a factor of at least x740. Dry weights (overall mean of plants in both sizes of pots) of both sycamore and birch were positively and significantly related to (i) total soil P (ii) extractable soil P, (iii) isotopically exchangeable P (iv) soil phosphatase activity and (v) extractable Ca (Table 21). In addition, growth of sycamore, but not that of birch, was related to pH and extractable K. In multiple regression analyses, the combination of soil phosphorus properties accounted for 72 and 80% of the variation in the growth of sycamore and birch respectively. Adding pH and extractable K in the analysis increased the proportion for sycamore to 87%. One soil (no. 3) contributed strongly to these percentages, but even when data for this soil were omitted, the growth of both species was still significantly correlated with soil phosphorus properties and, in the case of sycamore, with pH and calcium. However, as a consequence of omitting the data for soil 3, the growth of sycamore was found to be negatively correlated to (i) total N, (ii) extractable NH_4-N, (iii) loss-on-ignition and (iv) extractable iron. The relations with (i) and (ii) are difficult to comprehend at present but those with (iii) and (iv) might be expected, as they themselves are negatively related to pH.

These results indicate the over-riding importance of soil phosphorus to seedling growth so confirming earlier work done with soils from Cumbria and north Wales. Helliwell (1973) found that growth of sycamore and birch could be related neither to soil nitrogen nor extractable potassium; instead correlations with amounts of soil extractable phosphorus were significant and positive. More

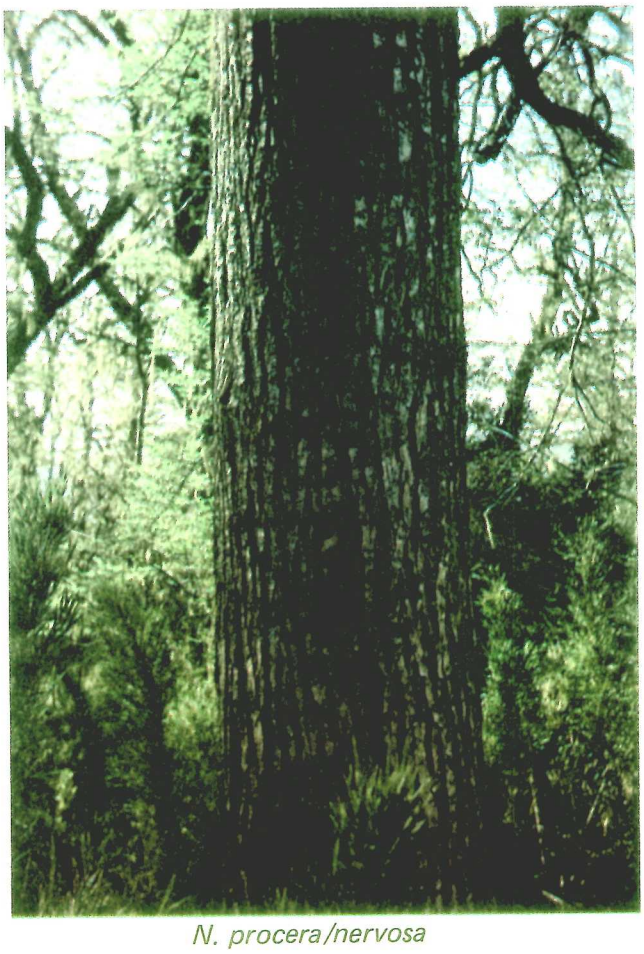
TABLE 21 Proportion of variation (r^2), accounted for when considering the production (g dry wt) of sycamore and birch in relation to soil chemical properties

Soil Properties	Sycamore	Birch
Loss-on-ignition	.02	.02
pH	(.52*)	.01
Total P	.44	(.75*)
Total N	.001	.09
Extractable P	.30*	(.70*)
Isotopic exch. P	.32*	.69*
Phosphatase activity	(.45*)	(.70*)
Extractable NH_4 -N	.10	.01
Extractable NO_3 -N	.09	.12
Extractable K	(.24*)	.001
Extractable Ca	(.40*)	(.35*)
Extractable Fe	.09	.01

* r^2 significant at $P < 0.05$

( ) = significant deviation from linear regression at $P < 0.05$

Plate 1 Hedges and hedgerow trees—the damage wrought to elms and the landscape by the aggressive strain of the Dutch elm pathogen, *Ceratocystis ulmi*. Photograph: Forestry Commission.



N. procera/nervosa

N. obliqua

Plates 2 & 3 *Nothofagus* spp.—will either of these South American species be grown on a large scale in Britain introducing diversity to the stock of plantation forests? Photographer: F T Last.

Plate 4 Cona Glen, Highland Region, Scotland. National Woodlands Classification: Type 28. Tree species: *Pinus sylvestris, Betula* spp. Ground vegetation: *Calluna vulgaris, Molinia caerulea.* Altitude *c.* 250m. Bedrock: Schist. Photographer: R G H Bunce.

Plate 5 Harrow Weald, Middlesex, England. National Woodlands Classification: Type 17. Tree species: *Betula* spp, *Quercus petraea.* Ground vegetation: *Deschampsia flexuosa, Pteridium aquilinum.* Altitude *c.* 140m. Bedrock: London clay. Photographer: F T Last.

Plates 6 & 7 These photographs illustrate the impact of trees in residential areas. The trees form a considerable resource which needs to be sustained. But is this being done? Are sufficient attempts being made to provide improved planting stock? Photographer: J E Good.

Plate 8 Majestic open-grown trees like this parkland oak can still be found but in decreasing numbers. More determined efforts should be made to characterise and analyse the range of variation within native trees. Photographer: J E Good.

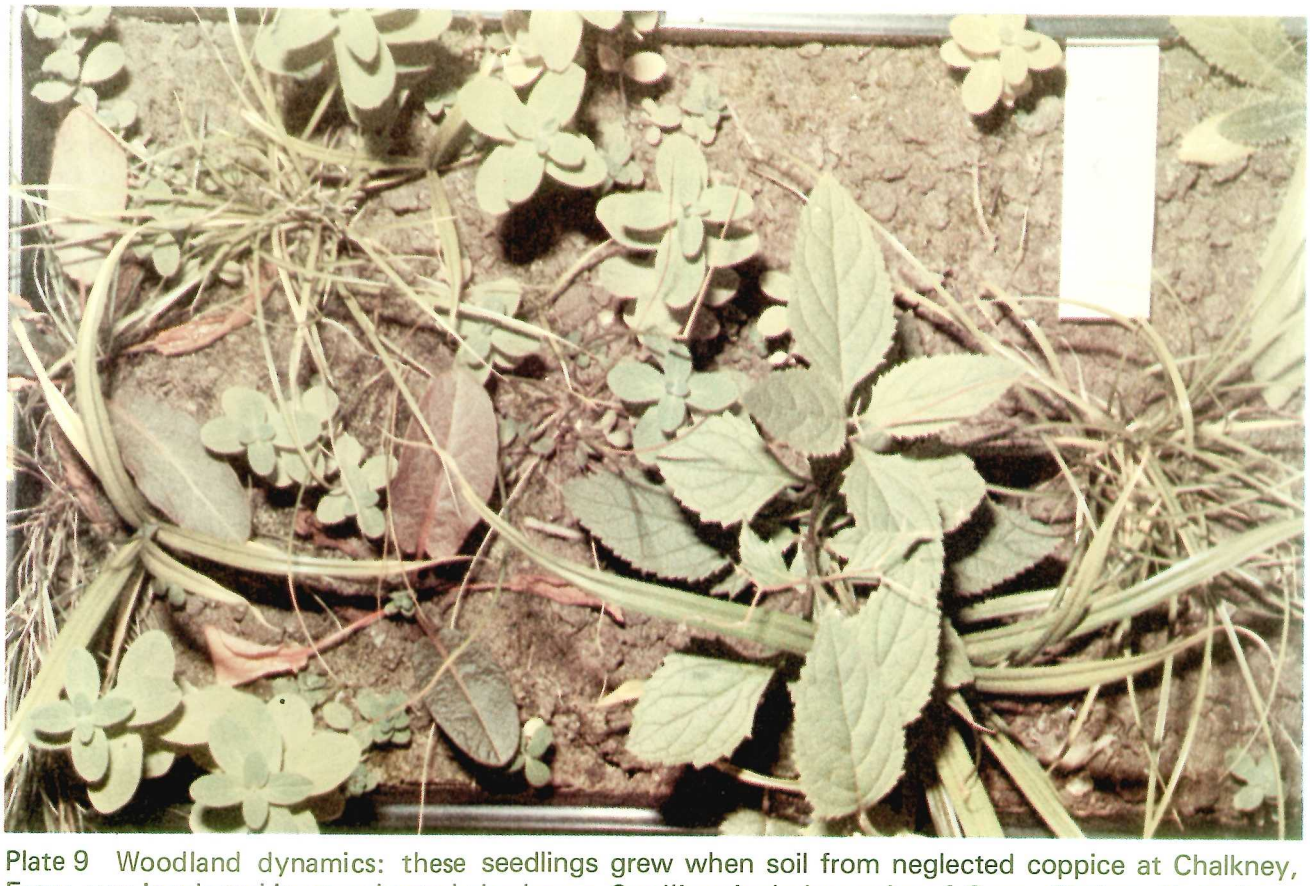


Plate 9 Woodland dynamics: these seedlings grew when soil from neglected coppice at Chalkney, Essex, was incubated in an unheated glasshouse. Seedlings include species of *Carex, Cirsium, Hypericum, Juncus, Poa, Rubus, Rumex* and *Scrophularia.* Photographer: A H F Brown.

Plate 10 Dunham Massey Park, Greater Manchester, in the spring: a pasture-woodland. Photographer: P T Harding.

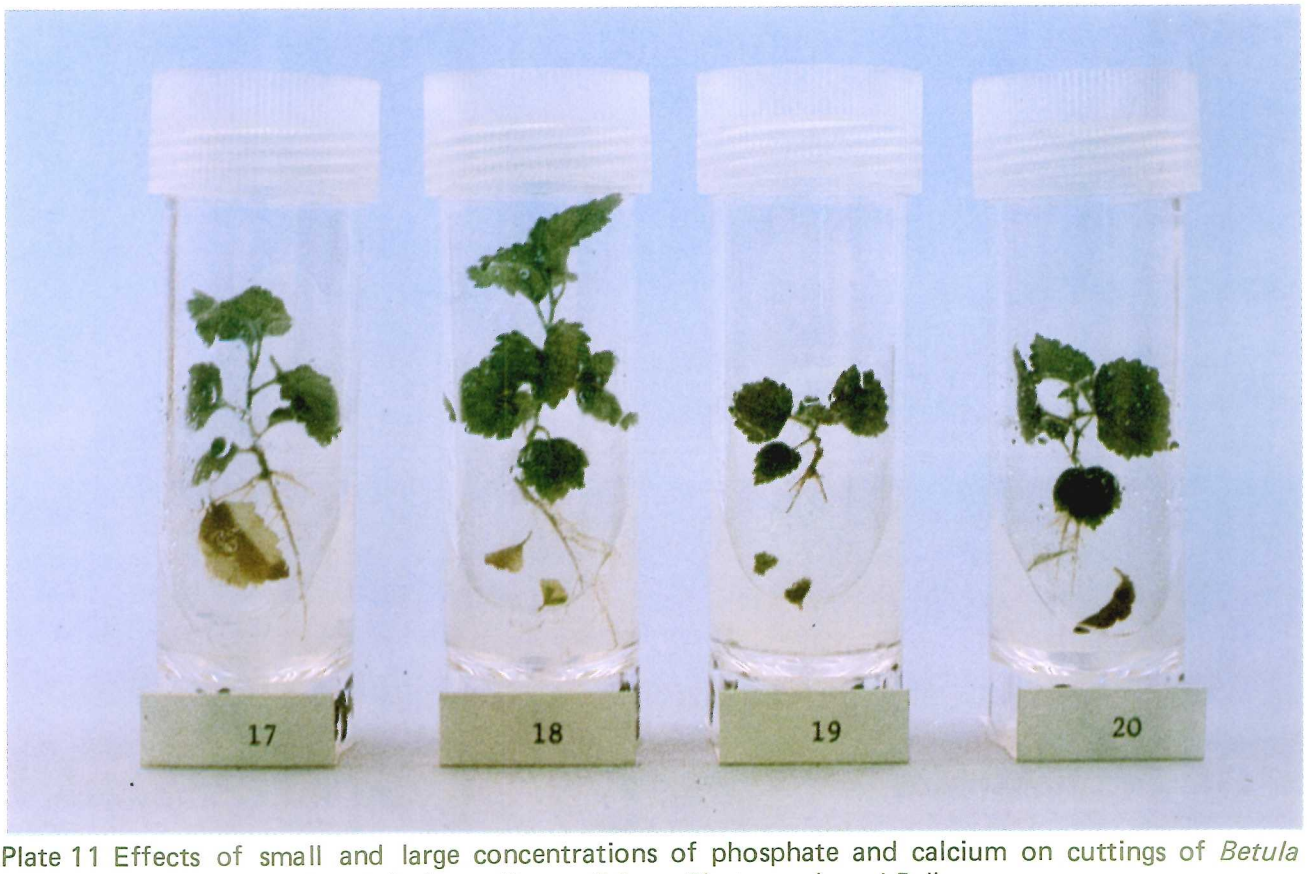


Plate 11 Effects of small and large concentrations of phosphate and calcium on cuttings of *Betula pendula* growing on nutrient jelly in sterile conditions. Photographer: J Pelham.

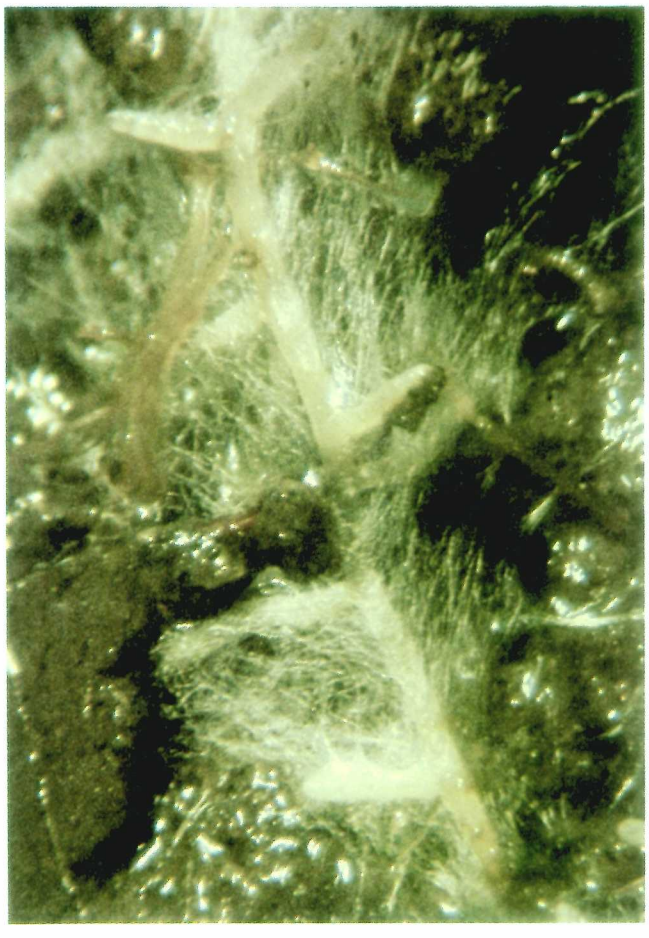


Plate 12 The stubby roots (mycorrhizas) formed when *Hebeloma* sp.—a fungus—colonises the roots of birch, *Betula* spp. Photographer: P A Mason.

Plate 13 Fruitbodies produced by mycorrhizal fungi in the autumn around a birch tree *(Betula pendula)*, about 8 years-old. The fruitbodies of *Leccinum rigidipes* are nearest the stem, those of *Hebeloma crustuliniforme* are the most distant, with those of *Lactarius pubescens* in between. Photographer: J Pelham.

Plate 14 Presumably it might be profitable to exploit these birch saplings, *Betula pendula,* which are successfully colonising an old coal tip. Have they innate tolerance which could be exploited by vegetative propagation? Photographer: J Wilson.

Plate 15 Flower induction in trees—the formation of cones by Sitka spruce, *Picea sitchensis,* 16 years-old; see front cover for flowers of *Triplochiton scleroxylon.* Photographer: E D Ford.

Plate 16 Characteristic crown of the West African timber tree *Triplochiton scleroxylon* growing in Nigeria. Attempts are being made to conserve the full range of variation found within this species. Photographer: F T Last.

Plate 17 One of the hazards sometimes encountered when vegetatively propagating: cuttings from lateral shoots of *Triplochiton scleroxylon* with leaves arranged in two rows (distichous) sometimes grow horizontally (plagiotropically), in contrast to the erect growth of cuttings with leaves arranged in spirals (polystichous). Photographer: R R B Leakey.

Plate 18 Transverse maternal gallery (with female present) and larval galleries burrowed beneath the bark of oak by the bark beetle *Scolytus intricatus.* Photographer: M G Yates.

Plate 19 Crotch feeding on oak, *Quercus robur,* by a female bark beetle, *Scolytus intricatus*—the wound is typically made at the junction between the current and preceding season's growth. Photographer: M G Yates.

Plate 20 A newly emerged white admiral, *Ladoga camilla,* which exploits areas of light shade abounding in neglected coppice. Photographer: J Grant.

Plate 21 Fifth instar larva or caterpillar, of the white admiral, *Ladoga camilla.* It feeds on honeysuckle which abounds in neglected coppice. Photographer: E. Pollard.

Plate 22 Grey squirrel, *Sciurus carolinensis.* Photographer: R D Kenward.

Plate 23 Bark stripping of sycamore attributed to grey squirrels. Photographer: R D Kenward.

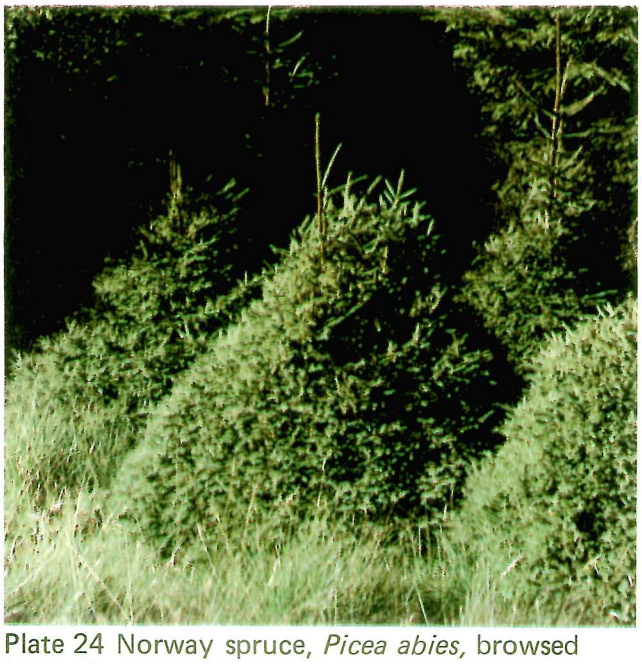


Plate 24 Norway spruce, *Picea abies,* browsed by red deer, *Cervus elaphus,* in Rannoch Forest, Perthshire. Photographer: B W Staines.

Plate 25 Bark stripping on lodgepole pine, *Pinus contorta,* by red deer, *Cervus elaphus,* in Glen Hurich, Inverness-shire. Photographer: B W Staines.

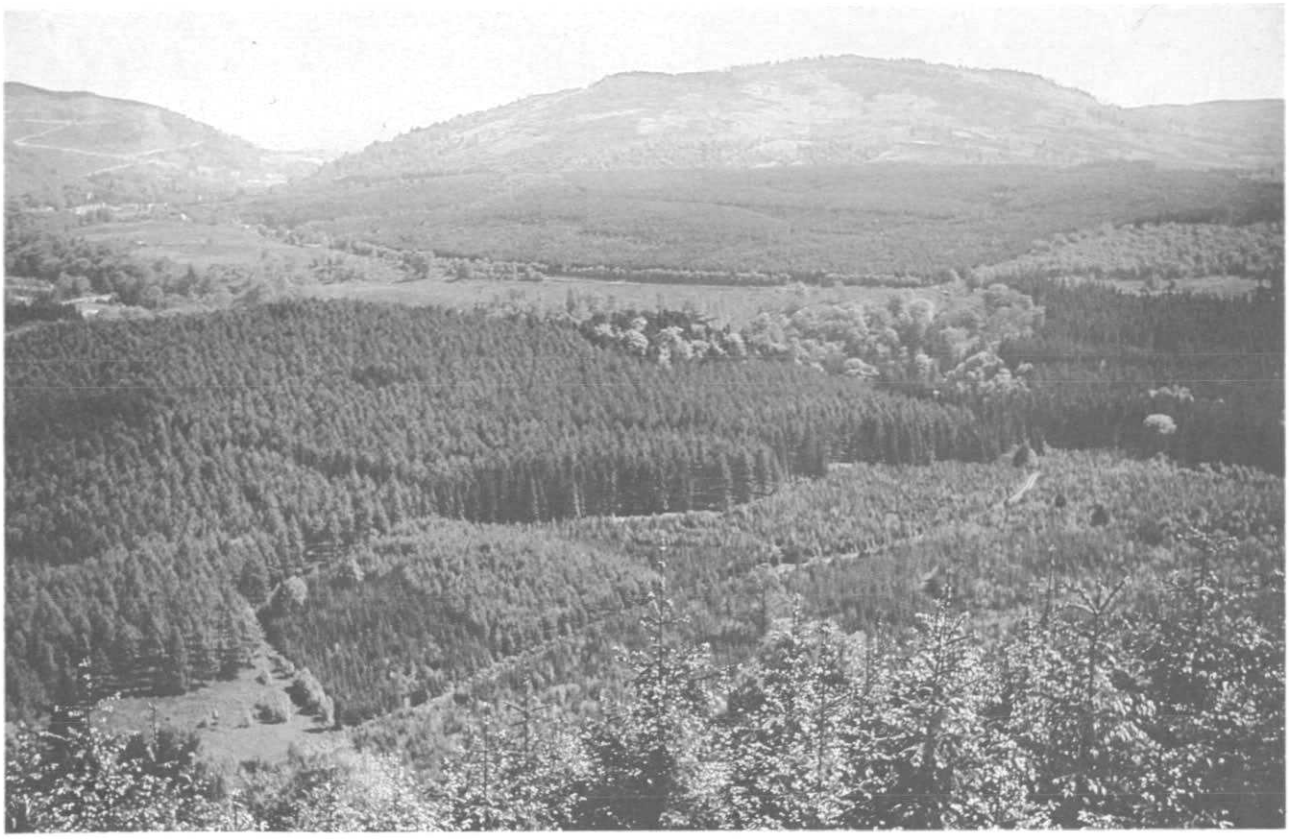


Plate 27 Ladywell plantation, Craigvinean, Scotland. Photograph: Forestry Commission.

Plate 26 Doirean na h-Earba, Compt. 297. Natural Scots pine, *Pinus sylvestris,* viewed from the south, Glengarry. Photograph: Forestry Commission.

recently the responsiveness of sycamore and birch to phosphate fertilizers was estimated using a bioassay technique based on the differential uptake of ^{32}P-labelled phosphorus (Harrison & Helliwell, 1979). These results parallel those obtained in production forestry where positive responses to phosphate fertilizers are commonplace (Zehetmayr, 1960; Everard, 1974; Binns, 1975). Nitrogen fertilizers can stimulate tree growth on heather-dominated sites except when heather has been killed by herbicide applications, but are otherwise usually of little value.

It was not surprising to find that sycamore grew badly on soils more acid than pH 3.9, this species preferring base-rich sites (Klotzli, 1970). On the other hand, one would expect the invasive birch to be more tolerant of low pH, but it too grew poorly on soils of $<$3.9 pH.

Clearly the production of sycamore and birch is dependent on phosphorus availability in soils. But what about other species of trees? How do the demands of tree species compare with those of other types of plants? Answers to these questions are being sought in a continuing programme of research, enlarged to study the responses of *Agrostis tenuis* and *Trifolium repens,* as well as birch, to 104 different soils of 8 pedological classes.

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17. NUTRITIONAL VARIANTS OF BIRCH

J. PELHAM and P.A. MASON

Insofar as they have been studied, trees, like other plants, vary greatly in their above ground form and behaviour and their responses to a variety of environmental factors. However, comparatively little is known of their response to different soils. Bearing in mind that many non-woody plants differ in their abilities to (i) take up and utilise nutrients and (ii) tolerate toxic concentrations of pollutants, as may be found on sites of dereliction, it would be surprising if comparable differences did not occur among trees. Tree nutrition should not be considered without reference to mycorrhizas, the intimate associations formed when fungi colonize roots sometimes causing gross changes in root morphology, eg the stubby roots developing as a result of colonization by sheathing (ecto-) mycorrhizal fungi. Because these associations have many features in common with root colonization by pathogens and symbionts, such as the nodule bacterium, *Rhizobium trifolii* Dangerd, of legumes, and because the success or failure of the latter is controlled by complementary genetical factors in the plant host and microbial colonizer, it was decided to add an investigation of the genetical factors controlling mycorrhizal formation to broaden a study of tree nutrition. For this work 2 of the 3 British native species of birch (*Betula pendula* Roth. and *B. pubescens* Ehrh.) were chosen because they are (i) widespread and contribute significantly to the landscape particularly of the uplands, (ii) fairly precocious and prolific producers of small seeds with few internal reserves, (iii) readily grown in axenic conditions more particularly as standard surface sterilants easily control the superficial microbes that contaminate the seeds, and (iv) propagated vegetatively without undue difficulty. Initially *Amanita muscaria* (L. ex Fr.) Hooker, the fly agaric, was chosen as the mycorrhizal associate because (i) it was already known to form sheathing mycorrhizas with birches both in 'the field' and controlled laboratory conditions, (ii) it is readily recognised, (iii) it grows adequately on laboratory culture media, and (iv) being a basidiomycete it opened the possibility of exploiting the series of well established techniques of genetic manipulation.

Because of the desirability of working in axenic conditions, seeds collected from birch trees growing on a wide range of sites were surface sterilized with hydrogen peroxide and germinated on water agar before being transferred to slopes of mineral nutrient agar in transparent polystyrene tubes with plastic caps (Pelham & Mason, 1978). The standard nutrient medium contained all the nutrients required for optimum growth as specified for birch by Ingestad (1971). Growth was increased by piercing the caps and plugging the resultant holes with cotton wool but was decreased by increasing the concentration of salts. To minimize variation attributable to genetic segregation in out-bred and variable populations of seedlings, a technique was developed for aseptic vegetative propagation. Single node cuttings, each with a leaf, were taken from seedlings 6-8 weeks old and placed on an agar medium containing minerals, sucrose and naphthalene acetic acid (NAA) so as to accelerate root production. The optimal concentrations of these additives were determined experimentally—none was essential (Table 22). The currently used rooting medium contains the nutrients specified

TABLE 22 Effect of 20 g/l sucrose and 1mg/l naphthalene acetic acid (NAA), singly and combined, on the rooting of birch cuttings when assessed after 17 days cultivation on either water or Ingestad's agar.

Substrate	% rooted	Mean root no. per cutting	Time of root emergence (days)
Water agar	6	0.1	11
+ sucrose	14	0.2	10
+ NAA	86	3.1	7
+ sucrose + NAA	64	3.0	7
Ingested agar	6	0.1	11
+ sucrose	25	0.3	10
+ NAA	93	5.1	6
+ sucrose + NAA	93	6.2	6

TABLE 23 Effects of different amounts of P on the growth of low phosphorus 'tolerant/intolerant' clones of *Betula pubescens* and *B. pendula* *.

Growth characteristic	Species of *Betula*	Low phosphorus 'tolerant' (mg P/l) 26.0	Low phosphorus 'tolerant' (mg P/l) 0.4	Low phosphorus 'intolerant' (mg P/l) 26.0	Low phosphorus 'intolerant' (mg P/l) 0.4	S.E.
Leaf area (cm^2)	*pendula*	8.8 *(2.17)*	8.0 *(2.08)*	7.9 *(2.07)*	3.5 *(1.25)*	*(±0.213)*
	pubescens	9.9 *(2.29)*	5.9 *(1.77)*	14.7 *(2.69)*	5.2 *(1.66)*	
Stem length (mm)	*pendula*	46.5 *(3.84)*	33.8 *(3.52)*	39.0 *(3.66)*	14.4 *(2.67)*	*(±0.098)*
	pubescens	41.2 *(3.72)*	30.4 *(3.41)*	41.4 *(3.72)*	13.9 *(2.63)*	
Root number	*pendula*	19.5 *(2.97)*	56.4 *(4.03)*	14.4 *(2.67)*	18.6 *(2.92)*	*(±0.328)*
	pubescens	9.4 *(2.24)*	51.6 *(3.94)*	29.8 *(3.40)*	39.3 *(3.67)*	

* For statistical analysis, estimates of growth (x) were transformed to $\log_e x$ (italicised figures).

by Ingestad (1971) supplemented with 0.1 mg/ l NAA and 10 g/l sucrose. Cuttings from the oldest and youngest nodes of a plant respectively grew significantly more and less rapidly than cuttings taken from intermediate nodes, a degree of variation that was acknowledged in experimental randomisations.

To allow experiments to extend beyond 8 weeks, plants have been grown aseptically using containers made by sealing a clear plastic beaker into the lid of a petri dish. A cotton wool plugged hole in the beaker assisted ventilation and the lid was sterilized by gamma irradiation. The modified lids were used to replace the conventional lids over plantlets already growing in petri dishes containing nutrient medium, thus providing more space for aerial growth. These containers and plantlets were grown at room temperature in cabinets lined with aluminium foil and continuously lit with fluorescent strip lights (Plate 11).

Synthesis of mycorrhizas was achieved by growing 10 day old birch seedlings on agar slants containing Ingestad's mineral nutrients plus glucose and thiamine hydrochloride (Mason, 1975). Each seedling was inoculated with a block of Hagem agar (Modess, 1941) culture of selected isolates of *A. muscaria* collected from birch and pine in Britain, India and the USA. The inoculated seedlings were incubated as described above for 6-8 weeks.

1. Results

By modifying the concentrations of different nutrients, it was possible to assess the growth capabilities of different clones. Between-clone differences were detected when 16 clones were grown in media with a decreased concentration of phosphate (P), but not when the standard concentration of phosphate was used. Thus, in an experiment with a pair of selected contrasting clones of each species the aerial parts of "low phosphorus tolerant" clones grew nearly as much with the smaller as with the standard amount of phosphate, whereas "low phosphorus intolerant" clones grew significantly less when phosphate concentrations were decreased (Table 23). In contrast, decreasing the concentration of phosphate increased root growth of "intolerant" plants slightly but greatly stimulated that of "tolerant" plants. Chemical analysis of the tissues of the 16 clones grown at standard and lesser phosphate concentrations showed that, although at low concentrations the amount of P (%) in the tissues was similar, there were considerable differences between clones and even between species when grown at the standard phosphate concentration. Differential responses also occurred when birch cuttings were grown on media with different concentrations of calcium.

The studies of nutrient response were extended to assess effects of 3 different concentrations of phosphate on the establishment of mycorrhizas by 6 isolates of *A. muscaria* (Table 24). Mycorrhizas were only formed by one isolate on a medium with the lowest concentration of phosphate, whereas 4 of the 6 formed mycorrhizas at higher concentrations.

At the optimum concentration (6.5 ppm P) both seed-lot and fungal isolate determined the number and branching of mycorrhizas. Moreover in an experiment in which 4 isolates were applied to 4 seed-lots, one isolate collected from beneath a spruce tree formed more mycorrhizas with 3 of the birch seed-lots than did either of the birch isolates (Table 25). The performance of the fourth isolate

TABLE 24 Effects of 3 phosphorus concentrations on the development of mycorrhizas when seedlings of *Betula pendula* (ex Scotland) were inoculated with 6 isolates of *Amanita muscaria.*

Cultures of *A. muscaria*		Presence (+) or absence (–) of mycorrhizas on *B. pendula* growing in media with different P concentrations		
Isolate	Origin	3.25 ppm	6.5 ppm	26 ppm
1	Britain *(Betula)*	–	+	+
2	Britain *(Betula)*	+	+	+
3	Britain *(Pinus)*	–	+	+
4	USA *(Pinus)*	–	–	–
5	USA *(Pinus)*	–	+	+
6	USA *(Pinus)*	Not tested	+	–

TABLE 25 Interacting effects of 4 isolates of *Amanita muscaria* and 4 seed-lots of *Betula pendula* on numbers of mycorrhizas on roots of seedlings.

Cultures of *A. muscaria*		Seed-lots of *B. pendula*			
Isolate	Origin	Q11	V21	W 5	W 2
7	Britain *(Betula)*	6.2	5.4	10.0	15.4
8	Britain *(Betula)*	14.2	14.8	20.6	18.4
9	Britain *(Picea)*	26.0	14.6	23.8	19.6
10	India *(Pinus)*	19.8	20.2	12.6	12.8

from beneath *Pinus pseudostrobus* Lindl. in southern India also indicates the ability of isolates of *A. muscaria* to infect other tree species.

Although the tubes used in these experiments severely limited the size of birch plants produced, *A. muscaria* considerably stimulated root growth in many experiments, the amount of increase being clearly dependent upon both seed-lot and isolate used. For example, 3 isolates each stimulated the numbers and total lengths of roots as compared with the uninoculated control, but to differing degrees (Table 26).

Inoculation with *A. muscaria* was also associated with significantly increased stem diameters in the colonized birch seedlings (Table 27). Inspection of transverse sections of stems under the microscope revealed that, in addition to altering the widths of the different tissues, inoculation also altered their fine structure (Mason *et al.*, 1977).

The most conspicuous changes in inoculated plants were (i) the accelerated development of bark and (ii) the stimulation of larger, more rounded cortical cells with intercellular spaces, differences that might enable mycorrhizal seedlings to be better "equipped" when planted in "stress conditions" of waterlogging or drought.

From the work done to date, it seems that the response within a species to added nutrients is variable. The value of this inherent variation in fitting a particular tree to a site and for increasing yield has yet to be determined, as has its inheritance and combining ability in breeding programmes. In the future, when the genetics of mycorrhizal systems are better known, it may be deemed necessary for the tree breeder to select, breed and multiply the fungal isolate best suited to the trees being bred. An extension of this work to some of the currently popular economic tree species and their associated fungi is being considered.

TABLE 26 Effects of 3 isolates of *Amanita muscaria* on the development (n) of roots of seedlings of *Betula pendula* (ex Scotland). Data were transformed to log (n + 1) for analyses; detransformed values in brackets.

		Growth of roots of *B. pendula*		
	Inoculation treatments	Number of roots per seedling	Total root length per seedling (mm)	Mean length per root (mm)
Isolates of *A. muscaria*	1	4.70 *(111)*	5.48 *(254)*	1.11 *(2.23)*
	2	4.48 *(91)*	5.43 *(241)*	1.28 *(2.61)*
	3	3.89 *(65)*	4.79 *(178)*	1.27 *(2.57)*
	Uninoculated control	3.60 *(46)*	4.29 *(105)*	1.13 *(2.11)*
Least significant difference (P = 0.05)		0.145	0.122	0.061

TABLE 27 Effect of inoculating roots of *Betula pendula* with the mycorrhizal fungus *Amanita muscaria* on the width of the different stem tissues.

Treatment	Width of stem tissues (μm)			
	Epidermis/bark	Cortex	Xylem/pith	Total
Uninoculated control	16	100	514	629
Inoculated with:				
isolate 11	100 *(530)*	121 *(22)*	543 *(6)*	765 *(22)*
isolate 12	85 *(430)*	138 *(38)*	604 *(18)*	827 *(31)*

Measurements were made on 3 sections of each replicate seedling. Figures in brackets refer to percentage increases.

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18. TOADSTOOLS AND TREES

P.A. MASON

Unlike those of annual and biennial plants, many of the smaller roots of coniferous and broadleaved trees are, as a result of colonization by mycorrhizal fungi, short and stubby. The identity of the different fungi would be difficult to determine if it were not for the production of conspicuous and characteristic fruitbodies, mostly toadstool-like, in the autumn. Having planted a plot of birch in July 1971, attempts have been made to analyse some of the factors influencing the production of (ecto-) mycorrhizal toadstools in succeeding years. The plot of ground at the Bush Estate (lat. 55°52'N) was divided into 3 replicate blocks each planted at 3 x 3 m spacings with 20 saplings (8 x *Betula pubescens* Ehrh.; 12 x *B. pendula* Roth) whose seed sources ranged from 66°30'N (Sweden) in the north to 50°40'N (S. Germany) in the south. 1974 the number of trees, out of 60, with toadstools increased from 13 to 38. At the same time mean numbers of toadstools per tree were twice as large around *B. pendula* as compared with *B. pubescens,* with a clear indication that more were associated with trees of southern than of northern origin. By 1975, the overall number of toadstool-producing fungi had increased to 5 but more importantly some had very distinctive patterns of distribution. For this reason it was decided to take the co-ordinates of all toadstools appearing during the autumns of ensuing years, hoping that their occurrence above ground may accurately reflect the development of mycorrhizas below ground (Figure 38). Observations made by Dr J.H. Warcup suggested that this was likely to be so but much more evidence is needed before the relation can be expressed quantitatively (Plate 12).

From 1975-1977, the annual production of sporophores increased steeply to more than 19,000 (Table 28) with the effects of seed origin becoming

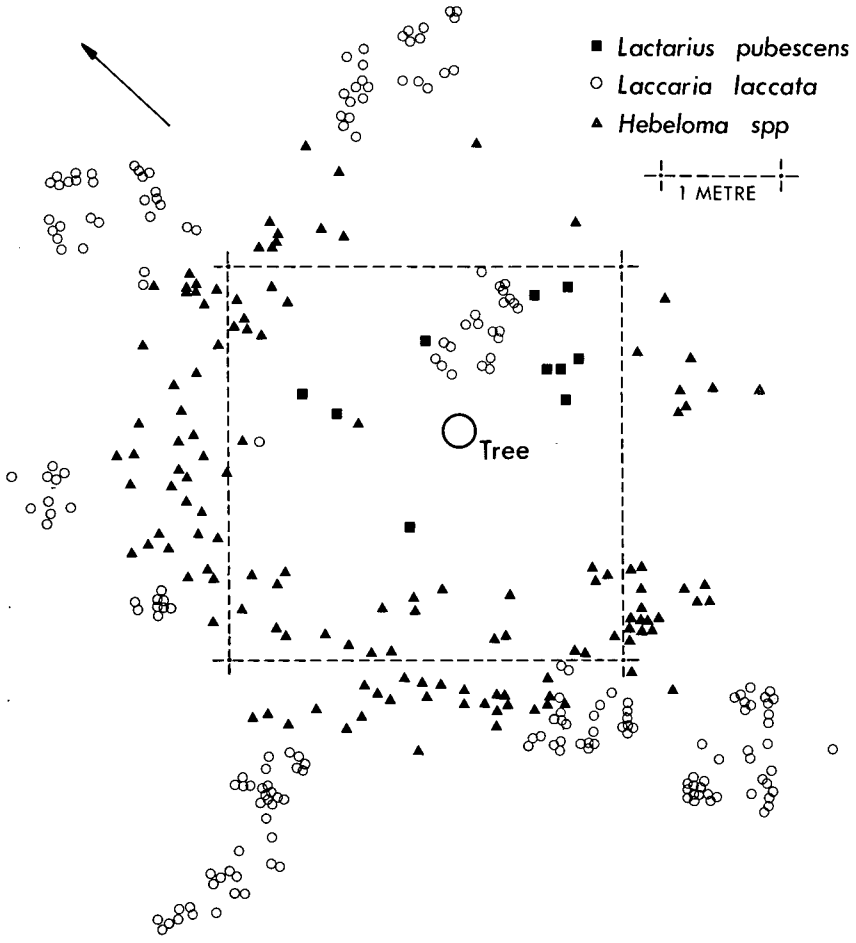

Fig. 38 *The distribution of mycorrhizal fungi around a sapling of* Betula pendula, *4 years after planting.*

A few toadstools of 2 species of fungi, known to form mycorrhizas with birch (Trappe, 1962), were observed near the saplings in 1973 with those of *Hebeloma crustuliniforme* (Bull. ex Saint Amans) Quélet being the more numerous. From 1973 to conspicuous. Eighty-one, 150 and 766 sporophores were produced per tree of southern origin (lat. 50°40'N) in 1975, 1976 and 1977 respectively, while only zero, zero and 3 were associated with those from the most northerly location. As leaves

TABLE 28 Changing populations of toadstools in an ageing stand of *Betula pubescens* and *B. pendula* planted in 1971 at the Bush Estate, near Edinburgh.

Observations made in	No. of trees (of 60) with toadstools	Nos. of fungal species	Annual production of toadstools	Mean nos. of toadstools/tree
1973	13	2	170	13
1974	38	3	680	18
1975	47	5	4900	140
1976	52	12	8500	160
1977	59	22	19000	320

Footnote: counts restricted to fungi known to form mycorrhizas with Betula spp.

of trees from northerly locations yellowed sooner than those from elsewhere, it seems that there is a link between the amounts of persistent foliage and toadstool production (Meyer, 1974).

In 1976 and 1977 numbers of different toadstool species associated with the plot of birch increased sharply to 12 and 22 respectively with as many as 9 being associated with individual trees. In addition to 7 species of *Hebeloma,* 3 species of *Leccinum,* 2 of *Laccaria* and one of *Lactarius* have been recorded. Interestingly, analyses of their location indicated that the spaces currently filled by toadstools had not been occupied in previous years by toadstools of the same or different species. This observation suggests that each fungus has its own particular niche in space and time which may be a product of competition between different species and/or dictated by the effects of the host and its environment. In the period from planting to the end of 1977, the mean distances of sporophores of *Hebeloma crustuliniforme* and *Lactarius pubescens,* from their tree 'hosts', had appreciably increased, but the 'rings' of the former were becoming increasingly fragmented. The significance of these changes and their relation to the occurrence of mycorrhizas in different parts of a root system is being further analysed. However, in the meantime, the effects, already mentioned, of foliage on the production of toadstools were confirmed when another batch of trees was artificially defoliated in 1978– sporophore production being interrupted more or less immediately. Whereas 'mycorrhizal toadstools' (6 or more per tree) were associated with 40 of 64 trees during August, only 2 in total developed in September after defoliation on 22 August, with none at all in October and November (Figure 39). When another batch of trees was defoliated on 25 July there was the same immediate response, but, in this instance, a new flush of leaves developed towards the end of September and, with it, a new crop of toadstools (Plate 13).

Bearing in mind the intimate contact between tree roots and mycorrhizal fungi it is not surprising that there is a degree of interdependence. It has been possible to identify a succession starting with *Hebeloma crustuliniforme,* followed successively by *Laccaria laccata, Lactarius pubescens* and *Inocybe* spp, then other *Hebeloma* spp and *Leccinum* spp. Should note be taken of this array of fungi in considering the choice of species when making artificial inoculations? Should *Hebeloma crustuliniforme,* the first in succession, be used or can the choice be widened? Is the succession attributable to the effects of earlier colonisers or is it, in the main, a reflection of the host's changing metabolism? Should we be thinking of a root system as a single entity or do different sections of it differentially favour the growth of the assortment of mycorrhizal fungi? We already have evidence to suggest that, when planted in the same soil, different seedlings of the same birch seed-lot may be selecting different mycorrhizal associates.

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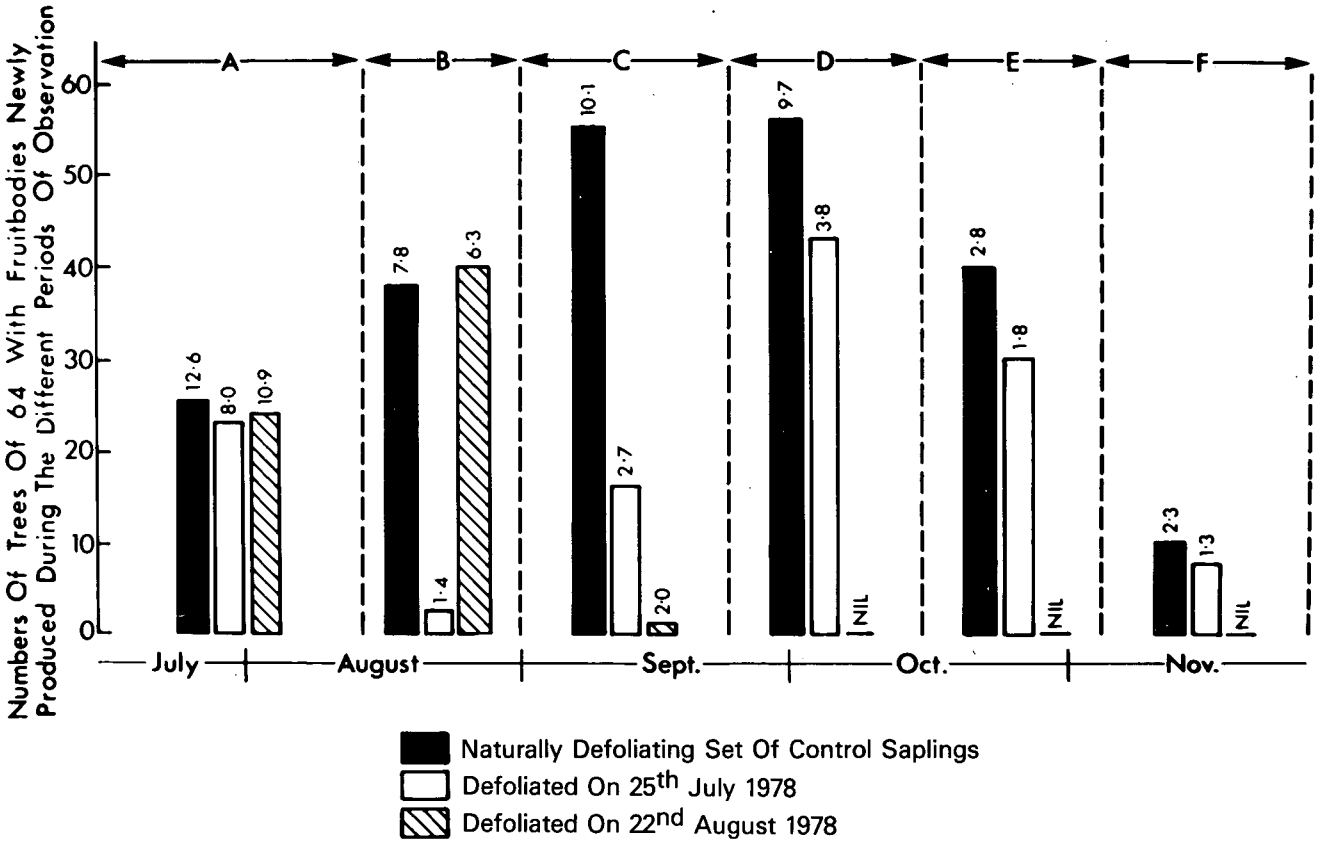

Fig. 39 *Mean effects of defoliating* Betula *spp on either 25 July or 22 August 1978 on numbers of replicate trees with fruitbodies of associated mycorrhizal fungi newly produced within the different periods of observation. (Figures at tops of columns are mean numbers of fruitbodies per tree produced during each period; they were calculated from replicates producing at least one new fruitbody during the relevant period.).*

19. EFFECTS OF TREES ON SOILS

J. MILES

Despite a considerable literature on the subject, there is very little substantive evidence about effects of different tree species on soils and soil processes. This lack of evidence is surprising, because the reputations of certain conifers for acidifying and creating podzols (Noirfalise, 1968), and of some hardwoods, notably birch, for ameliorating podzols (Gardiner, 1968) suggest, if true, profound implications for forestry practice and land use in the uplands.

Accordingly, a study was begun in late 1973 to identify the trends, rates, limits and causes of soil changes associated with birch development on poor moorland soils. This paper summarises the main findings to date, and then discusses three topics whose general importance has become increasingly apparent as the study proceeded: the consequences of soil changes, the role of roots in soil changes, and the effects of forestry management practices on nutrient availability.

1. Effects of birch

Thirteen sites situated from Sutherland to north Yorkshire are being studied. At each site, soils under first generation birch stands of different ages are being compared with soils in immediately adjacent areas without birch. Two of the sites are old quarry floors in moorland, 3 are felled Scots pine stands planted on former heather moorland, while the other 8 are on heather moorland. *Betula pubescens* predominates at 3 of the sites, and *B. pendula* at the others. The degree of uniformity of soil and vegetation over each site before birch colonization began was assessed by examination of soil mineralogy and particle size distribution, soil profiles, and buried stem fragments, viable seed and pollen. This examination provided the background against which present differences could be interpreted.

Since birch colonization, substantially the same trends seem to be evolving at all sites although the extent and rate of change vary considerably between sites. (Table 29 shows some of these trends at one site.).

TABLE 29 Soil analyses from heather moorland and nearby stands of *Betula pendula*, aged from 18 to 90 years old, Advie, Morayshire, Scotland.

		Age of *B. pendula* stands				
	Heather moorland	18 years	26 years	38 years	90 years	LSD at 5% level
* pH	3.8	3.9	4.0	4.7	4.9	0.1
**Exchangeable H (mg dm^{-3})	117	108	109	101	89	25
**Exchangeable Ca (mg dm^{-3})	196	201	207	489	319	83
**Total P (mg dm^{-3})	151	210	196	240	232	82
**N mineralization after 14 days incubation (mg dm^{-3} $week^{-1}$)	−1.3	25	41	45	40	10
**C/N ratio	30	26	19	22	15	11
**C/P ratio	500	320	280	270	170	200
**C/K ratio	440	430	410	460	310	210
**Bioassay: mean shoot dry weight (mg) of 8 weeks old radishes.	8.7	18	43	59	66	18
Mean number of earthworms per 1 m^2 (by formalin extraction)	1	5	27	127	78	26
***Extractable Fe (mg 100 g^{-1})	173	125	670	590	640	530
***Extractable Al (mg 100 g^{-1})	128	150	375	520	480	632

* Soil from 0-5 cm, after removing L + F layer.

** Soil from 0-15 cm, after removing L + F layer.

*** Soil from the bottom 10 cm of the A horizon.

1.1 Vegetation changes:

a) Gradual death of the *Calluna* ground cover as birch canopies develop, and it is replaced by *Deschampsia flexuosa* and *Vaccinium myrtillus* in particular, the former especially on more mineral soils, the latter where an organic surface horizon is better developed.

b) Gradual appearance of species characteristic of woodlands and grasslands, eg *Agrostis* spp, *Anthoxanthum odoratum, Hypericum pulchrum, Oxalis acetosella, Viola riviniana,* as soil conditions change.

1.2 Soil changes:

a) An early decrease in suitability of the ground as a seed bed follows changes in the field layer, but there are indications of a later improvement, possibly associated with increased concentrations of large herbivores attracted to the changed swards.

b) A gradual change takes place in the composition of the buried seed flora to one characteristic of woodland; soil pollen accumulations change similarly.

c) There is a considerable increase in numbers of surface living earthworms, especially *Lumbricus rubellus,* with *Lumbricus terrestris* and *Allolobophora* spp appearing later as soil conditions change.

d) There is a gradual breakdown of the old *Calluna* mor humus layer and its conversion to a mull-like form, probably due largely to earthworm feeding.

e) Increased rates of organic matter decomposition and of nitrogen mineralization are recorded.

f) There is a decrease in exchangeable hydrogen, but increases in pH, exchangeable calcium and total phosphorus.

g) There is a decrease in carbon/nitrogen, carbon/phosphorus and carbon/potassium ratios from the critical levels present on the moorlands (*c*20-30, 350-500 and 400-500 respectively) at which nutrient immobilization and deficiencies would be expected (Evers, 1967; Gosz *et al.,* 1973; Dowding, 1974).

h) Growth of test plants (radish, *Luzula sylvatica* and *Rumex acetosa*) increases in bioassay trials.

i) A suggestion that the bleached Ea horizon in podzols was being gradually obliterated by the incorporation of organic matter and ferric iron, thus tending to form brown podzolic profiles.

The work has raised many questions; 2 in particular are being investigated:

(i) What is the origin of the increased amounts of calcium found in the topsoil of relatively old stands of birch? Through its effect on pH, this calcium seems to be critically involved in the change from mor to mull. Initially, it was suggested that birch may be absorbing calcium at greater depths than heather, but, while this is being investigated, current evidence suggests that birch is also accelerating the weathering of soil minerals throughout the profile as compared with heather.

(ii) If depodzolization does occur under birch, how is the Ea horizon obliterated? Soil mixing is probably the major cause. If so, to what extent can this be attributed to earthworms, other soil living animals and to the growth of roots?

To verify the soil changes inferred from this survey, and to elucidate further the mechanisms involved, a series of long term experiments is being established. Birch is being planted at 3 heather moorland sites on podzols, and heather is being established after felling birch at 3 sites with brown podzolic soils. With the information gained it is hoped that a more complete and meaningful model of the soil processes involved can be made.

2. Consequences of soil changes

Unlike birch and many other broadleaved species, many conifers are typically associated with mor humus systems (eg pines and spruces) with (i) relatively slow rates of organic matter decomposition and nutrient release, (ii) considerable immobilization of nutrients in the soil organic matter, and (iii) soil acidification and, in susceptible soils, accelerated podzolization (Miles, 1978). What are the consequences of these changes under conifers compared with those under mull-forming broadleaved species?

Because podzols and mor humus systems are generally associated with poorer volume growth of trees, even of species adapted to such conditions, than are brown podzolic soils and mull humus systems (Lag, 1962; Pyatt, 1970; Page, 1971), it might be expected that soil changes under conifers would eventually cause declining yields. But the evidence is equivocal. Whereas some studies have indicated slower growth rates of second generation stands of conifers at some sites (Siren, 1955; Keeves, 1966; Whyte, 1973), others have been unable to detect changes (Genssler, 1959; Holmsgaard *et al.,* 1961; Hausser, 1964; Bublinec, 1973).

However, because the faster rates of decomposition and nutrient release associated with broadleaved trees in mull-forming systems would be expected to accelerate plant growth, would an admixture of broadleaved trees benefit the growth of conifers? There have been claims to this effect (Shumakov, 1958; Kovalev, 1969; Blintsov, 1971; Prudic, 1972), but the supporting data are unconvincing. The value of pure versus mixed stands clearly needs critical examination. In much of Britain and the rest of western Europe, soils developed under natural broadleaved woodland have now been replanted with conifers. Remembering that in natural conditions soils are commonly subject to a succession of tree species, while indeed in boreal regions like much of the Scottish highlands, conifers and broadleaved species tended to alternate, should we be considering rotations of species in these plantations? Or has their need been obviated by the ubiquitous use of ploughing and the increasing use of fertilizers? The answers are as yet unknown.

3. The role of roots in soil change

Because of the technical difficulties involved, many important questions about the influence of roots on soil processes remain unanswered, eg:

3.1 What is the relative importance for different tree species of different parts of the profile, including the litter layers, as zones of nutrient uptake?

3.2 How do roots and mycorrhizas affect the weathering of mineral particles and the availability of particular nutrients?

3.3 To what extent do roots, mycorrhizas and rhizosphere microbes influence nitrogen availability by inhibiting nitrification (Moore & Waid, 1971; Rice & Pancholy, 1972, 1973), stimulating nitrogen fixation (Richards, 1964, 1973; Richards & Voigt, 1964), and utilizing organic, and possibly also organically bound, forms of nitrogen (Fisher & Stone, 1969; Lundeberg, 1970; Stribley & Read, 1974)?

3.4 To what extent do mycorrhizas stimulate (Bjorkman, 1970) or inhibit (Gadgil & Gadgil, 1971) organic matter decomposition?

3.5 To what extent do roots alter the balance of soil resources and transfer materials over distances by contributing exudates and moribund tissues, whether whole roots or plates of cells, by causing mechanical disturbance, and through the influence of root grafts? What are the effects of these processes on nutrient cycling and availability?

4. Effects of management practices on nutrient availability

Of these, ploughing and harvesting are of outstanding importance. In nature, soils are 'ploughed' through the effects of growing root systems and of soil-living animals, and as a result of disturbances when trees are uprooted by wind. These processes cause *inter alia* the downward movement and fragmentation of surface accumulations of organic matter, and the upward movement of deeper lying, relatively unweathered, nutrient rich mineral particles. However, these are rarely the reasons for ploughing as a preparative site treatment. Nonetheless its effects on nutrient cycling should be known and related to those of natural soil mixing. The latter is a gradual process, with the associated mobilization of nutrients probably being more or less balanced by their uptake by plants. In contrast, ploughing as a management technique is abrupt and grossly disruptive. It is likely to cause a surge in nutrient mobilization, with the products being in excess of the requirements and absorbtive capacity of the surviving vegetation, resulting in possibly substantial losses of essential nutrients from the system. On infertile soils these losses may have long lasting effects on tree growth (Van Goor, 1954).

Removal of trees has 2 contrasting effects. On the one hand it accelerates the decomposition of soil organic matter and the mineralization of nutrients (Wright, 1957; Wells & Jorgensen, 1975), and this may be reflected in increased tree growth (Haberland & Wilde, 1961). On the other hand, loss of trees deprives the system of a considerable accumulation of nutrients. Rennie (1955) thought that their repeated loss from nutrient poor soils would eventually reduce tree growth, but he overlooked the accession of nutrients to the system from the atmosphere and from mineral weathering, and his fears were ignored at a time when the addition of fertilizers to make good soil nutrient deficiencies was becoming more general. However, nutrient losses may assume greater importance if whole tree harvesting, with the removal of branches and major roots, were to become accepted practice (Malkonen, 1974; Nilsson & Wernius, 1976), and even more so if needles and leaves were also used (Alestalo, 1974; levins *et al.*, 1974). There could be serious repercussions on the cycling of nutrients, also queries about the wisdom of spending larger sums on the replacement of nutrients whose manufacture is energy-demanding. The subject warrants re-examination. How much tree growth can be sustained on particular site types with natural or achievable rates of nutrient cycling, nitrogen fixation and mineral weathering, with the additional help of beneficial mycorrhizas?

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Within-species variation and its genetical control

20. *BETULA PUBESCENS*—THE AFFINITIES OF TYPES IN THE SCOTTISH HIGHLANDS WITH THOSE OF CONTINENTAL EUROPE: A STUDY OF LEAF MORPHOLOGY OR THE APPLICATION OF MORPHOMETRICS

A.S. GARDINER

Of the 3 species of *Betula* L. native to Great Britain, one is the dwarf birch, *B. nana* L., whereas the other 2, *B. pendula* Roth, the silver birch, and *B. pubescens* Ehrh., the downy birch, form medium sized trees. *B. pubescens* is the more variable of the latter, it being current practice to subdivide it into 2 subspecies. Subspecies *pubescens* is believed to be more widely distributed in lowland habitats, whilst ssp *odorata* is associated with the Scottish highlands.

Instead of 2, 3 subspecies of *B. pubescens* are recognised in continental Europe—ssp *pubescens,* ssp *tortuosa* and ssp *carpatica.* It may appear at first glance that ssp *odorata* is unique to Britain, but a closer comparison of the various editions of the Flora of The British Isles with Flora Europaea shows that ssp *odorata* has been equated at different times with both ssp *carpatica* and ssp *tortuosa.*

Because of their variability ssp *carpatica* and ssp *tortuosa* have only been distinguished with difficulty. They are essentially shrub-like mountain or highland birches; ssp *tortuosa* has the more twisted appearance with many interlacing branches and ssp *carpatica* is the less hairy or pubescent. In an attempt to define these variable subspecies more clearly, Jentys-Szaferowa (1950) made a biometric study of their leaf sizes and shapes. On the basis of population means for a set of 13 continuous variables, she derived species means for *B. pendula (B. verrucosa), B. pubescens, B. carpatica, B. tortuosa, B. obscura and B. oycoviensis,* the subspecies already mentioned being given specific ranking within a broader concept, the collective species *B. alba* L.

Her variables included different characteristics that determine both leaf size and shape. Thirty to 40 years ago the analysis of the data was time-consuming and restricted, but, with the advent of electronic computers and more sophisticated statistical packages, the task has been made easier and more searching, notably through the use of principal component analysis.

With these advances it was decided to (i) investigate the differences between mainly highland samples of *B. pubescens* and (ii) seek their affinities with their continental counterparts, remembering that British populations, which originally migrated from the continent, have now been isolated for thousands of years.

1. Objectives

1.1. To obtain the relevant portions of Jentys-Szaferowa's data so as to structure a comparison between British populations of *B. pubescens,* with special emphasis on those from the Scottish highlands, and their continental counterparts.

1.2 To determine if the observed differences among British populations are commensurate with a classification of 2 or 3 subspecies.

1.3 To detect if the patterns of variation among British subspecies are regionally distributed.

1.4 To study the range of variation of individuals within different populations. Do different discrete populations contain more than one subspecies?

2. Approach

Observations were made on leaves of (i) 23 mainly highland populations of *B. pubescens* identified and collected in 1953 by Dr F.W.J. England, (ii) 50 individual trees in Morrone National Nature Reserve and (iii) 15 trees from Sluie Wood—both Sluie and Morrone NNRs being located in Deeside, Scotland.

Although Jentys-Szaferowa used 13 continuous variables per leaf, this number was reduced to 6 by applying Jolliffe's method for discarding superfluous variables (Jolliffe, 1972, 1973). The compositon of this set of 6 changed slightly with modifications to the comparative framework (described below); those selected for the 3 taxa level are illustrated in Figure 40.

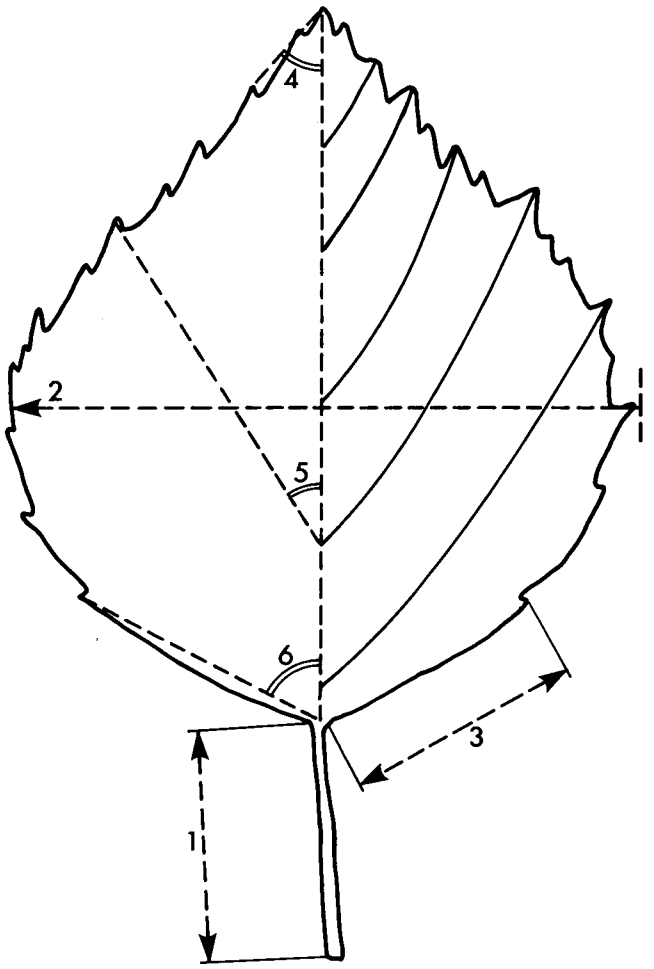

Fig. 40 *Diagram showing the 6 variables (selected by Jolliffe's method for discarding superfluous variables) which characterise the leaf morphology of* Betula pubescens *spp* pubescens, tortuosa *and* carpatica:
1. petiole length
2. broadest width
3. distance of 1st tooth from join of lamina and petiole
4. apex angle
5. axil of second nerve
6. angle at base of lamina.

The data were then subjected to principal component analysis, which indicated that the variation could be summarized by 2 significant axes or components. In the event, 3 principal component analyses were made—each preceded by a run of Jolliffe's procedure—in which numbers of taxa in the basic framework were reduced from 5 to 4 and, finally, 3. At the start, Jentys-Szaferowa's mean values for *B. pendula, B. pubescens, B. tortuosa, B. carpatica* and *B. oycoviensis* were included, *B. obscura* having been discarded as earlier work had shown it to be identical with *B. pendula* (Gardiner & Jeffers, 1962). In the second analysis, *B. pendula* was excluded as none of the 23 British populations showed a close affinity with this species; for a similar reason *B. oycoviensis* was dropped from the third analysis. In the third analysis, the first component contrasted the apex angle with the other variables and the second component contrasted blade width, apex angle,

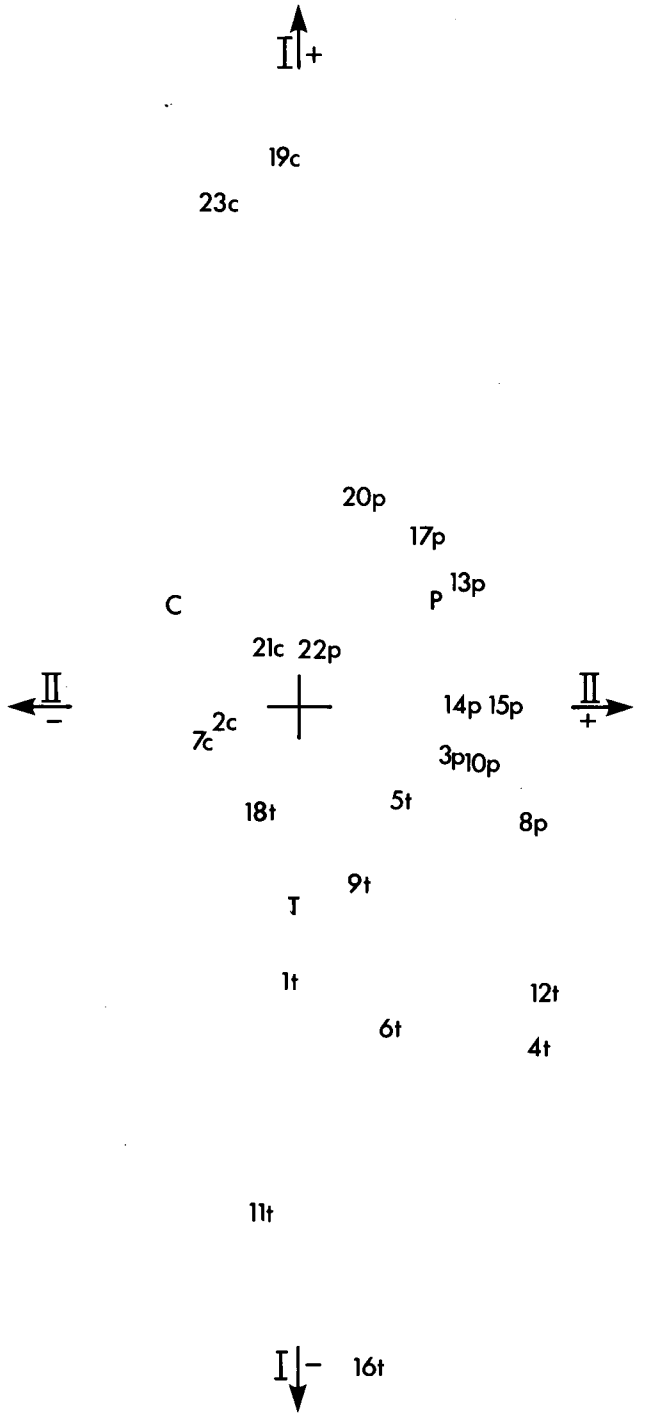

Fig. 41 *Distribution of 23 populations of predominantly Scottish* Betula pubescens *when the first (I) and (II) components of a principal component analysis, including details of continental spp* pubescens *(P),* tortuosa *(T) and* carpatica *(C), were arranged 2-dimensionally. c, p and t indicate affinities of the British populations (1-23).*

TABLE 30 Subspecies affinities of 23 British populations of *B. pubescens* when compared with (i) *B. pendula, B. pubescens, B. tortuosa, B. carpatica, B. oycoviensis* - 5 taxa; (ii) 4 taxa (*B. pendula* excluded); and (iii) 3 taxa (*B. pendula,* and *B. oycoviensis* excluded).

Sample No.	Location of British populations	Levels of comparison		
		5 taxa	4 taxa	3 taxa
1	Skye	carpatica	carpatica	tortuosa
2	Skye	pubescens	pubescens	carpatica
3	Loch Carron	pubescens	pubescens	pubescens
4	Achnasheen	tortuosa	carpatica	tortuosa
5	Achanalt	pubescens	pubescens	tortuosa
6	Tomatin	tortuosa	carpatica	tortuosa
7	Tomich	pubescens	pubescens	carpatica
8	Invergarry	pubescens	pubescens	pubescens
9	Glen Shiel	pubescens	pubescens	tortuosa
10	Bridge of Brown	pubescens	pubescens	pubescens
11	Cluanie	tortuosa	tortuosa	tortuosa
12	Newtonmore	oycoviensis	pubescens	tortuosa
13	Arisaig	pubescens	pubescens	pubescens
14	Kinlochleven	pubescens	pubescens	pubescens
15	Crianlarich	pubescens	pubescens	pubescens
16	Aberfeldy	tortuosa	tortuosa	tortuosa
17	Callander	pubescens	pubescens	pubescens
18	Penicuik	carpatica	carpatica	tortuosa
19	Houghton	carpatica	pubescens	carpatica
20	Hackness	carpatica	pubescens	pubescens
21	Ling Gill	carpatica	carpatica	carpatica
22	Borden	carpatica	carpatica	pubescens
23	Okehampton	pubescens	pubescens	carpatica

base angle and the axil of the second nerve with the remaining linear variables. These contrasts effectively separated *B. tortuosa* from *B. carpatica* and *B. pubescens* on the first (I) axis and *B. carpatica* from *B. pubescens* on the second (II) (Figure 41).

3. Outcome

When the 23 populations of *B. pubescens* were related (shortest Euclidean distance) to progressively fewer of the taxa, as defined by Jentys-Szaferowa, it was found that the affinities of some of them changed (Table 30). Thus, for example, the Skye population No. 1 seemed more like the continental *B. carpatica* when data for *B. pubescens, B. tortuosa, B. carpatica* and *B. oycoviensis* were included; when *B. oycoviensis* was excluded, the 3 taxa analysis suggested *B. tortuosa.* With the Skye population No. 2 there was a change from *B. pubescens* to *B. carpatica.* The analyses suggest that the 23 populations should be divided, as on the continent, into 3 subspecies *pubescens, carpatica* and *tortuosa,* the graphical representation of their distinctiveness, based on leaf characteristics (Figure 41), suggesting that the variation is continuous. Surprisingly, the 3 types do not seem to have disparate patterns of geographical distribution, there being a marked overlap between ssp *pubescens* and ssp *tortuosa* in the Scottish highlands (Figure 42).

TABLE 31 Affinities with *B. pubescens* ssp *pubescens, tortuosa* and *carpatica* of individual trees sampled in Morrone and Sluie Woods, Deeside, Scotland, when data were subjected to principal component analysis using reference data from these 3 subspecies.

	ssp. *pubescens*	ssp. *tortuosa*	ssp. *carpatica*	Number in sample
Morrone		50		50
Sluie	3	7	5	15

As with the populations, the affinities of the different collections of individual trees changed to some extent as numbers of European taxa used in the principal component analyses were progressively decreased. In 3 taxa comparisons (ssp *pubescens, tortuosa* and *carpatica*) all 50 trees in the Morrone NNR sample were most closely related to ssp *tortuosa,* but specimens of the other 2 subspecies, in addition to ssp *tortuosa,*

were identified at the lower altitude Sluie Wood, some 30 miles along the River Dee from Morrone (Table 31 and Figure 43). It seems therefore that the 3 subspecies may occur in the same region, but their occurrence may differ locally with changes of habitat and altitude. In some locations the additional presence of *B. pendula* may, through the ease of inter-specific hybridization, give rise to further variants.

The analyses have indicated that samples of pubescent birch, mainly from the Scottish highlands and, by implication, representatives of ssp *odorata,* have close affinities with the continental ssp *pubescens, tortuosa,* and *carpatica.* While these similarities suggest that a re-examination of their taxonomic status might be rewarding, there is little doubt that they refute the idea of regionally distinct subspecies.

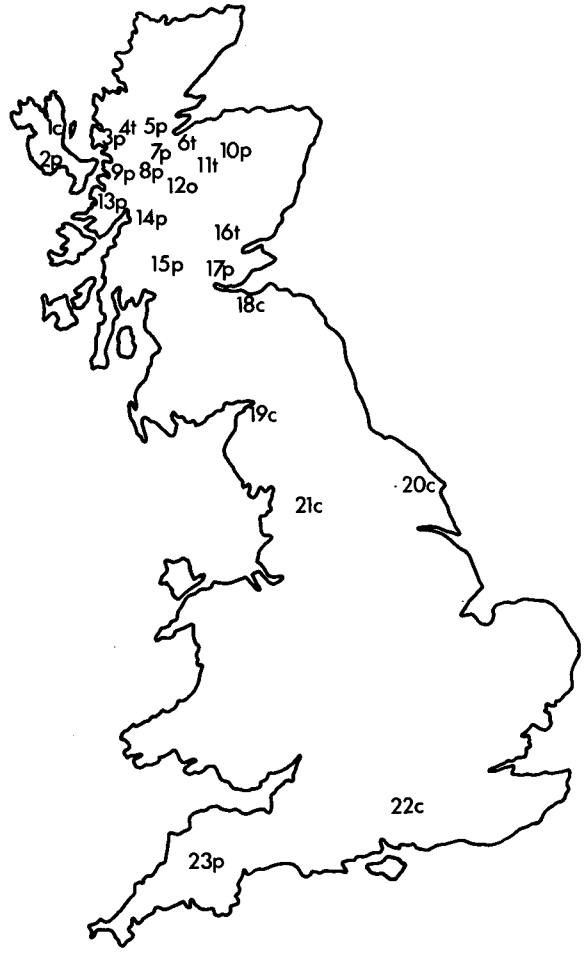

Fig. 42 *Geographical locations of 23 British populations of* B. pubescens *with their affinities at the "5-taxa level"* (pendula, pubescens, tortuosa, carpatica, oycoviensis). (*p* = pubescens, *t* = tortuosa, *c* = carpatica, *o* = oycoviensis).

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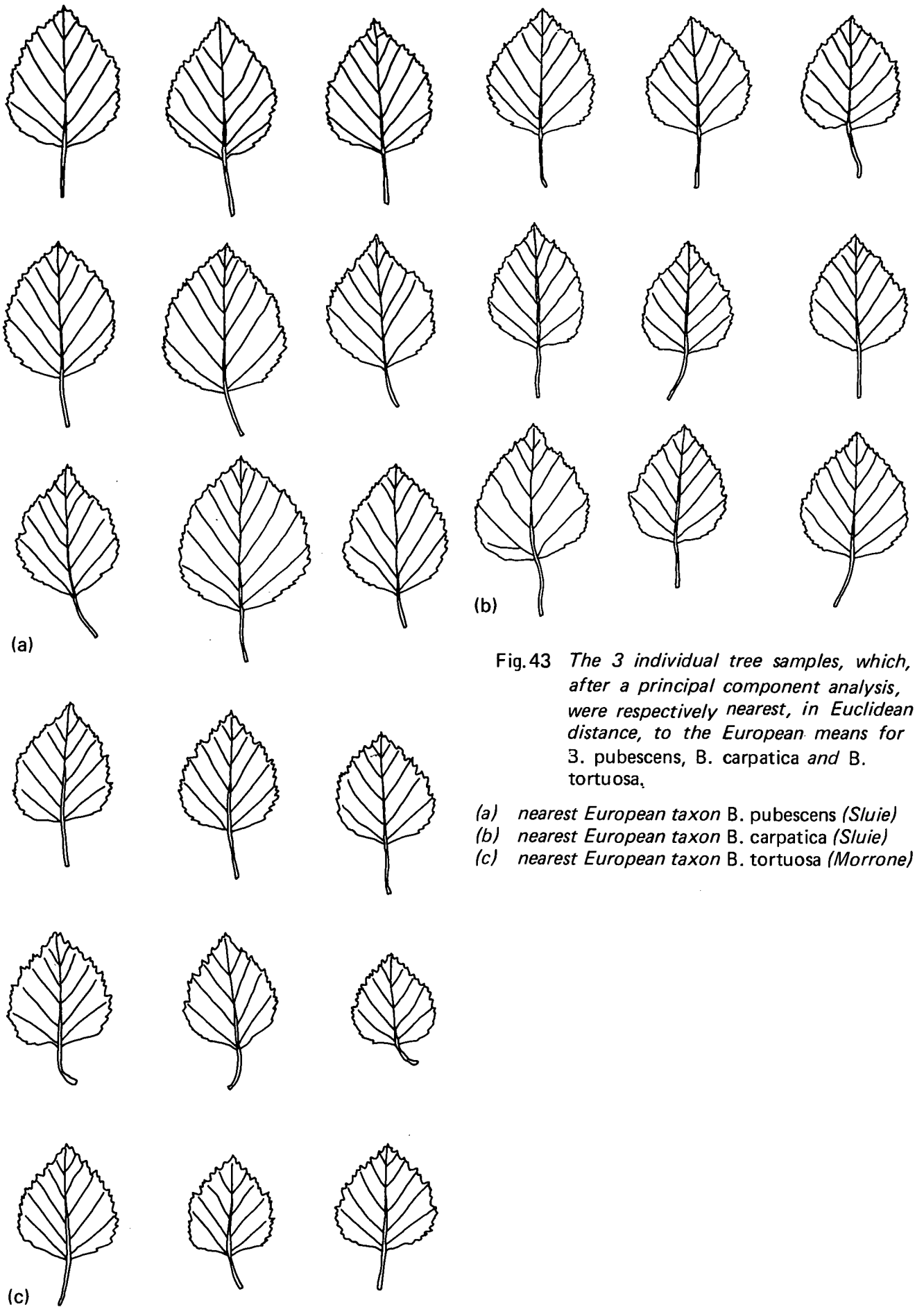

Fig. 43 *The 3 individual tree samples, which, after a principal component analysis, were respectively nearest, in Euclidean distance, to the European means for* B. pubescens, B. carpatica *and* B. tortuosa.

(a) nearest European taxon B. pubescens *(Sluie)*
(b) nearest European taxon B. carpatica *(Sluie)*
(c) nearest European taxon B. tortuosa *(Morrone)*

21. ANALYSIS OF THE VARIATION WITHIN SITKA SPRUCE, LODGEPOLE PINE AND LOBLOLLY PINE

M.G.R. CANNELL and C. CAHALAN

Unlike most agricultural crops, forest tree species are genetically not far removed from their wild progenitors, and are only just beginning to be domesticated. Whereas genecologists study patterns of natural variation in native species, ecophysiologists are more concerned with physiological and morphogenic processes which underly that natural variation. What is the physiological basis of forest tree yield? What yield-determining processes offer the greatest opportunities for genetic improvement? And how can these processes be identified and exploited by tree breeders?

Attention has been devoted, in the main, to the 2 most important commercial tree species in Britain, Sitka spruce (*Picea sitchensis* (Bong.) Carr.) and lodgepole pine (*Pinus contorta* Dougl.) which grow native over a wide area in western North America, and are genetically very heterogenous. Some work has also been done on loblolly pine (*Pinus taeda* L.) in the southern USA, where tree improvement work is more advanced. Work being done in ITE on Sitka spruce and lodgepole pine complements that of the Forestry Commission, which is gaining information empirically on the field performance of different provenances and elite-tree progenies of these species.

1. Research needs and approaches

There are 3 ways in which knowledge of yield physiology can aid tree improvement. Foremost, it should help define early selection criteria. Obviously, tree breeders cannot afford to wait for final harvest to evaluate genotypes, and the sooner inferior genotypes can be rejected, or superior types exploited, the more cost-effective the breeding programme. Second, physiologists can help breeders define 'ideotypes' (ideal plant types), determine whether these ideotypes are in practice being selected, and help plan crosses between complementary parents to produce the ideal combinations of attributes. Third, physiological understanding can help prevent errors of judgement and indicate what is possible. Are opportunities for genetic gain being missed, or being overrated?

Genetically different populations of trees have been grown by ITE and the Forestry Commission, and attempts have been made to analyse the nature of inherent growth differences. These analyses have contributed information of 3 kinds. First, they have provided a more complete description of differences in height growth by analysing its less complex components and subcomponents. Second, the analyses have provided some understanding of how particular phenotypes result from the interaction between growth components, and between genotypes and environments. Third, by analysing differences among provenances, open-pollinated progenies, controlled-cross progenies and clones, we have automatically obtained some information on the patterns of variation and inheritance of various attributes.

2. Descriptive analyses of the components of growth

Yields of field crops have been characterised in terms of numbers of ears, grains per ear, weight per grain, etc. The annual height increments of conifers can be analysed in a similar way.

2.1 Leader length = length per flush x numbers of flushes

Unlike *Pinus taeda,* which can produce 4-5 flushes per year in Arkansas, northern pines, and most mature north temperate spruces, produce only one flush of growth per year from an overwintered preformed bud. But, young *Picea sitchensis,* for instance, can produce second flushes, called 'lammas' or 'free' growth (see Figure 44). Young progenies, prone to produce second flushes, were found to grow outstandingly well at good sites and poorly at poor sites, an adaptation worth exploiting on good sites but not elsewhere (Cannell & Johnstone, 1979).

2.2 Length per flush = length per stem unit x numbers of stem units

A stem unit is a node plus internode in the strict sense—a needle plus its associated section of stem. The total annual complement of stem units produced by a conifer shoot is equal to the total number of primordia produced at the shoot apical meristem. When there is only one spring flush of growth from an overwintered bud, shoot growth is said to be 'predetermined', because all primordia were produced during the previous year. Inherent variation in the length of the single spring flush produced by provenances and progenies of lodgepole pine is attributable, almost entirely, to differences in numbers of primordia already present in the overwintering buds. That is, it is associated with the activity of the apical meristems during the previous year rather than with the extent to which the preformed shoots elongate Cannell *et al.,* 1976). However, in Sitka spruce there is additional inherent variation in the extent to which the preformed stem units elongate, and

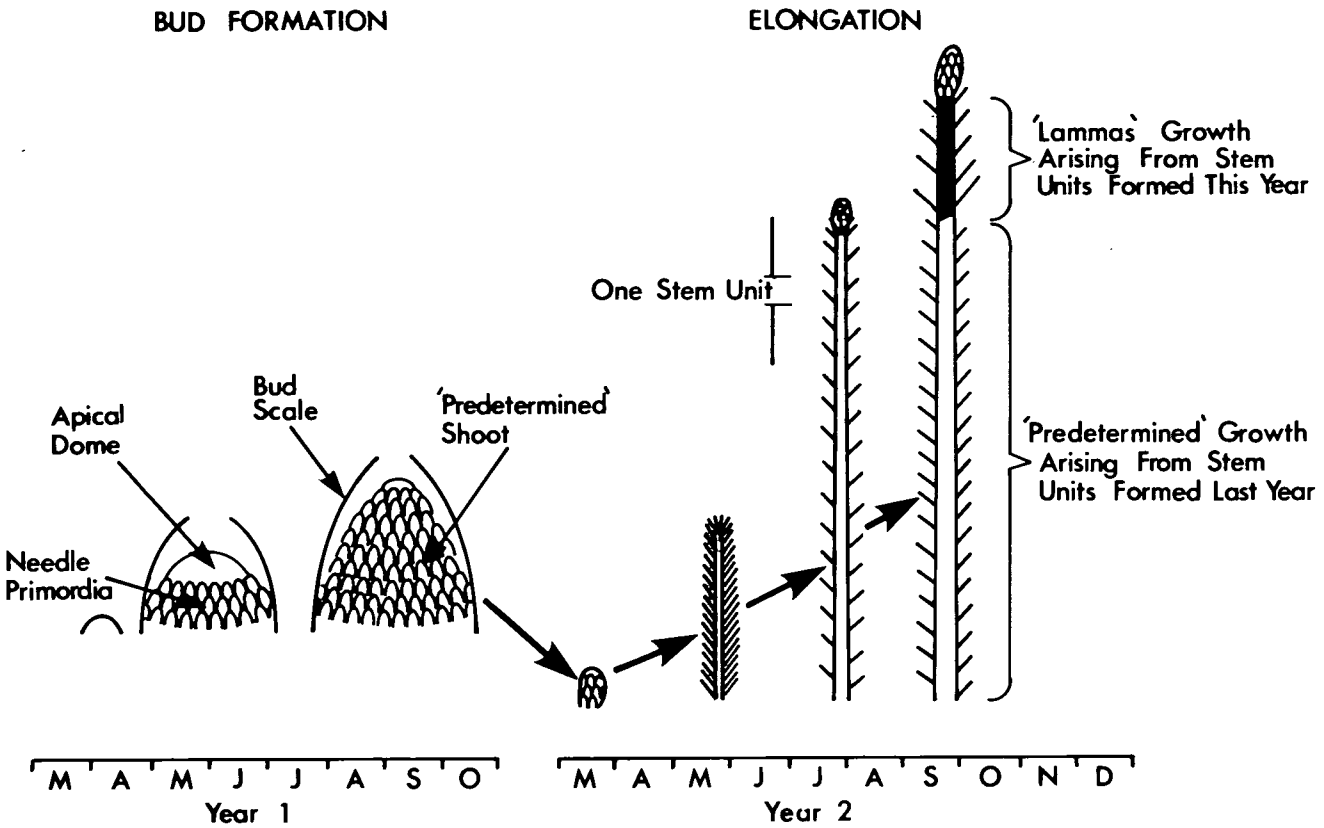

Fig. 44 *Stages in the development of the leading shoot of Sitka spruce.*

in loblolly pine there is inherent variation in stem unit elongation on the long second flush.

2.3 Length per stem unit = numbers of cells x length per cell

Observations suggest that differences in lengths of stem units result primarily from differences in cell numbers, set up during the early stages of shoot elongation, rather than from differences in the extent to which cells elongate (Baxter & Cannell, 1978).

2.4 Numbers of stem units = duration of stem unit initiation x rate of initiation

Because the number of preformed stem units is an important, and somewhat neglected, variable in conifers, detailed studies were made of stem unit initiation by following the seasonal activity of shoot apical meristems of different genotypes: apical meristems become active before bud-burst, and remain active long after bud-set. The seasonal duration of initiation was found to be important in all species examined, especially the prolongation of activity into late summer and autumn (Cannell & Willett, 1975).

In lodgepole pine, inherently different rates of primordia production at shoot apices are also important. These rates depend on the sizes of primordia relative to the size of the apical domes, and also on mean cell generation times.

2.5 Sizes of apical domes, sizes of primordia, and mean cell generation time

A technique was developed to estimate the transverse growth rates of apical dome tissues and the sizes of primordia (Cannell, 1976). Making certain assumptions, it was possible to show that the average time taken for cell numbers to double at conifer apices was in the range 40-120 h, as in many herbaceous plants. But conifers can produce primordia exceptionally rapidly (up to one per hour) because they develop large apical domes (up to 1.6 mm diameter) and very small primordia (only 2-5% the size of the apical domes). There are, however, complex seasonal fluctuations in cell division rates, dome sizes, and primordia sizes. The most important factor affecting the amount of new tissue generated is the size of the apical domes—large domes are equipped to produce more cells per cycle of cell division than small domes. Curiously, very little evidence could be found for inherent differences in maximal rates of cell division. An important feature distinguishing genotypes of *P. contorta* and *P. sitchensis* was the rate at which they enlarged their apical domes in spring (Cannell & Bowler, 1978), possibly reflecting differences in the efficiency with which metabolites were supplied to, or utilized by, the apical meristems.

3. Analyses providing understanding of growth relationships and environmental responses

3.1 Branching and tree growth

The growth of young conifers is limited by the rate at which they can build up their foliage biomasses. Genotypes differ in this respect, not only because of differences in the growth of their individual shoots (analysed above) but also because of differences in branching. Each shoot produces branches in proportion to its own length and this proportion differs among genotypes. For instance, provenances of lodgepole pine have from 0.25 to 0.35 branches per cm of parent shoot whereas provenances of Sitka spruce have from 0.60 to 0.85 per cm. These differences are the cause of large differences in branchiness, needle biomass production and early dry matter production per tree when combined with differences in shoot growth. Trees with long shoots (leaders and branches) will produce many laterals, sub-laterals and so on, whereas trees with short shoots will build up their foliage biomasses much more slowly. Using a simple model, it was found that slow-growing individuals of an otherwise fast-growing provenance could mimic members of an inherently slow-growing provenance (Cannell, 1974).

3.2 Dry matter distribution

Are there inherent differences in the functional relationships between shoots and roots (allometric relationships)? How are these related to observable patterns of shoot growth? Are they reflected in differences in root:shoot weight ratios which may influence wind stability? Differences in root: shoot allometry were not found among provenances of Sitka spruce and lodgepole pine, but may be important in progenies of loblolly pine (Cannell *et al.*, 1979). However, inherent differences occur in seasonal patterns of dry matter distribution between shoots and roots. Briefly, genotypes which stop increasing in height early in the growing season (although they may continue bud development late into the autumn) develop relatively large, heavy root systems by the end of the year. This root:shoot 'imbalance' is 'corrected' the following spring, but is set up again in the autumn and may influence the wind stability of trees during winter (Cannell & Willett, 1976).

3.3 Photoperiod, temperature and stress responses

Many of the genotypic differences already described are linked with differences in response to photoperiod, temperature and water stress. Thus differences between genotypes in their propensity to produce late-summer growth are probably related to their responses to day length. In contrast, differences in the seasonal duration of apical meristematic activity probably have more to do with temperature responses. More information is needed on the onset and loss of frost hardiness in relation to (i) shoot apical activity and elongation, and (ii) the frost hazard in different British upland regions. Water stress responses may also be important—not surprisingly, they proved to be crucial to the success of genotypes of *P. taeda* in the southern USA (Cannell *et al.*, 1979).

4. Patterns of variation and inheritance

Studies of Sitka spruce provenances have confirmed their essentially clinal pattern of variation with latitude of origin in western North America. Lodgepole pine has a more discontinous pattern of variation, with distinct differences in branching and physiology betweeen coastal and inland populations, suggesting that coastal x inland hybridization might be profitable.

Variation among progenies of elite trees of Sitka spruce is being analysed. Also the inheritance of some traits is being assessed on (i) Forestry Commission controlled-cross experiments, where physiological complementation may explain some instances of hybrid vigour, and (ii) ITE clonal trials which are revealing a high degree of within-provenance genetic variation in traits which were formerly thought to be poorly inherited.

5. The future

Practical seedling screening procedures, which can be used by tree breeders to evaluate progeny differences, are required to (i) minimize the need for long-term field testing, and (ii) shorten the generation time. Additionally, more needs to be known about the inheritance of the different components of growth. Also, work is needed to test the assumption made by tree breeders that fast-growing individuals will produce fast-growing forests (Cannell, 1979).

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22. WITHIN-SPECIES VARIANTS OF TREES FOR PLANTING DERELICT LAND

J. WILSON

Approximately 36,000 ha of the UK are classified as derelict, of which *c* 11,000 ha are attributed to the dumping of coal waste (Tandy, 1975). Natural colonization of this waste is usually a lengthy process, taking up to 80 years, with woodland ultimately developing on stable areas. To hasten this process, methods of reclamation have been developed, involving the addition of organic and artificial fertilisers, limestone, and occasionally top soil prior to sowing grasses and/or planting trees. Although these procedures are usually costly, success cannot be guaranteed. For the future, it would seem advisable to adapt these methods, taking greater note of the processes of natural colonization and reducing the reliance on ameliorants. Attempts are being made to obtain within-species variants of different species of trees that are adapted to conditions on derelict land and investigations of mycorrhizal associations of trees on these sites are in progress. For the future, the inclusion of leguminous plants such as broom and lupins is worth considering because of the ability of these plants to fix nitrogen.

1. Nature of substrate

Colliery waste is variable material and hence problems of reclamation vary from site to site. It is composed of varying proportions of mudstones, shales, siltstones, sandstones, seat earths (fireclays) and limestone characteristic of the geological strata associated with the different coal seams. In addition to reflecting the proportions of these different constituents, the physical and chemical nature of coal slag reflects the degree of weathering and the extent of burning.

The limited growth of plants on coal spoil can be attributed to at least 13 factors, but the relative importance of each of them varies from site to site and depends on whether or not the land has been regraded (Table 32). Nutrient deficiencies, extreme pH and compaction seem to be the most important factors limiting growth on regraded sites. Coal waste usually contains little or no nitrogen or phosphorus available for plant growth and acid shales are calcium-deficient. Iron pyrites is present in many wastes and can be the cause, when oxidised, of extremely acid conditions allowing the release of toxic amounts of aluminium and manganese. Acidity tends to increase as a result of weathering (Doubleday, 1971); surface materials, immediately after regrading, are typically neutral, tending to become acid in succeeding years. In Lancashire, pHs ranging from 2.2 to 7.9

TABLE 32 Some factors limiting plant growth on coal spoil

1. Physical factors
   - 1.1 instability and erosion
   - 1.2 unfavourable water regime
   - 1.3 absence of fine material
   - 1.4 compaction
   - 1.5 exposure
   - 1.6 spontaneous combustion
   - 1.7 extreme surface temperature
2. Nutritional factors
   - 2.1 nutrient deficiency
3. Toxicities
   - 3.1 extreme pH (range 2-10)
   - 3.2 extreme salinity
   - 3.3 presence of toxic metals
4. Biological factors
   - 4.1 absence of soil microbes and fauna
   - 4.2 lack of humus

have been recorded (Vyle, 1971). Compaction, caused by heavy earth-moving machinery, which can exert pressures of 49 kg cm^{-2}, has sometimes been so severe that penetrometer readings for regraded spoil have been the same as those for tarmacadam roads (Richardson, 1975).

2. Amelioration

In the short-term, raw colliery waste can often be ameliorated to give "instant" green fields. In these circumstances, the costs of amelioration and grassing can account for 30% of the £2,470-24,700 spent on reclaiming each hectare (1978 prices from the Scottish Development Agency). Large amounts (756 kg ha^{-1}) of nitrogen and phosphate-rich fertilisers are necessary plus limestone to counteract acidity—1% FeS_2 (pyrites) necessitating the application of 40 tonnes of limestone per hectare to neutralise the acidity of the top 15 cm layer of waste. It is usual to 'rip' the surface to minimise compaction before these amendments are applied. However, despite these procedures, it is still necessary to consider aftercare because of continuing acidity and the rapid leaching of nitrogen and the binding, in the absence of organic matter, of phosphate and potassium in inaccessible forms.

3. Plant selection

To make site amelioration more cost effective, and in the hope of minimizing the extent of aftercare, attempts are being made to refine the selection of trees grown on unameliorated coal spoils. Traditionally, plants are selected on the basis of their yields, disease resistance and ease of propagation, to mention but a few of the criteria. However, for planting spoil, often in exposed conditions, other criteria are likely to be of greater significance, remembering that trees that perform well on natural soils are unlikely to be those that tolerate spoil—they have not been subject to the selection pressures exerted by this unnatural substrate.

Bradshaw (1952), and subsequently others, working with grasses, have found that plants collected from metalliferous mine sites could tolerate larger concentrations of particular metals than 'normal' populations. Specifically, they have been able to identify populations of *Agrostis* spp, *Festuca* spp, *Anthoxanthum odoratum,* and *Holcus lanatus.* Mine spoil populations of grasses are tolerant of the metals that are present in normally toxic concentrations in wastes on which they grow; they are not tolerant of other metals. When 2 metals; (eg Pb, Zn) occur together in toxic concentrations, dual tolerances can be found. Jowett (1959) found that a lead-tolerant population of *Agrostis tenuis* was able to grow in substrates with amounts of calcium and phosphate which would have been inadequate for most populations—a suggestion of multiple tolerances. Salt tolerance has been found in *Senecio vulgaris* growing in roadside verges 'salted' during winter (Briggs, 1978); acid tolerance has been found in barley (Stolen & Andersen, 1978).

Tolerances that have been demonstrated so far have been confined to a few chemical factors, but plants growing on coal waste are subject to a multiplicity of adverse factors, chemical, physical and biological (Table 32), and, because some specimens of a variety of trees including species of *Betula, Sambucus, Salix* and *Quercus* seem able to establish themselves 'naturally' on some coal spoils, it seems likely that they may possess multiple tolerance unless one factor is of overriding importance. Two species of birch, *Betula pendula* and *B. pubescens,* and two of alder, *Alnus glutinosa* and *A. incana,* are being investigated; birch, because it is a primary coloniser, and alder, because nitrogen is fixed in its root nodules. *Alnus* spp have been used successfully in the reclamation of mining spoils in Denmark, Germany, Great Britain, Holland and the United States (Plate 14).

Working on the principle that trees growing successfully on coal waste may have tolerance, cuttings were taken from (i) natural colonizers and (ii) the better survivors of man-made plantings. Samples of soil taken from near their roots were analysed. During the last 2 years stocks of vegetatively propagated plants have been accumulated and are now being used in a series of glasshouse and field trials with commercially available nursery-stocks as the standards for comparisons—the 'controls'. During propagation, the roots of *Betula* spp are inoculated with soil containing inocula of mycorrhizal fungi; roots of *Alnus* spp are inoculated with a suspension of macerated root nodules. The field trials are being done on a variety of coal spoils with pH ranging from 5-7, growth being assessed with and without added fertilisers. So far, drought has been a problem, particularly on coarser wastes. In these conditions, some of the selected alder clones seem to be growing better than the controls (unselected nursery stock), their better performance possibly, and surprisingly in this genus, being related to drought tolerance.

On looking at fungal sporophores occurring on spoil heaps, it seems that improvements might be obtained if mycorrhizal inocula were taken from the heaps themselves where *Paxillus involutus* and *Scleroderma* spp, which are known to form mycorrhizas with many tree species, commonly occur (see Marx, 1975). These fungi contrast with species of *Hebeloma* and *Laccaria* which develop as a result of inoculation with nursery soil. Are *Paxillus involutus* and *Scleroderma* spp, or some isolates of them, inherently suited to conditions in industrial spoil?

4. Discussion

In doing this type of work, there is an 'unconscious' selection of rapid-growing 'easy-to-root' clones (as stocks of these build up more rapidly), a trait possibly running counter to the selection of tolerance; grasses adapted to small concentrations of nutrients are also slow-growing (Jowett, 1959; Gemmell, 1977). However, there is some evidence of tolerance in some *Alnus* clones and an impression that this tolerance may be largely related to their abilities to withstand drought. Early experiments have, however, served to emphasize the need to work on a broad front. Marx (1975) demonstrated that inoculation with effective mycorrhiza enhanced the establishment of some trees on strip-mined coal waste in Kentucky. Paralleling the search for tolerant trees, attempts are being made to ensure that mycorrhiza established during propagation will withstand conditions in coal spoil and tolerant strains of mycorrhizal fungi are being sought.

The use of nitrogen-fixing plants is an attractive alternative to the provision of fertiliser. *Alnus* spp are already being studied, both in their own right and as nurse plants for other species of trees.

However, the use of herbaceous nitrogen-fixers could also provide useful continuing nitrogen supplements minimizing the onset of growth checks attributable to nitrogen deficiencies. Doubtless, the readily available stocks of legumes could, for this purpose, be improved by selection, because it should be remembered that many grow badly on acid mine waste, possibly as a result of manganese toxicity and phosphate deficiencies (DoE Contract Report DGR1 B71, 1978). However, natural populations of gorse and broom seem to have no difficulty in establishing themselves, at least on some types of spoil.

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Flowering and vegetative propagation

23. POSSIBILITIES OF CONTROLLED REPRODUCTION IN TREES

K.A. LONGMAN

Knowledge of the developmental physiology of woody plants is very incomplete, and nowhere are the gaps more noticeable than with the reproductive responses of forest trees. Primarily this can be attributed to the scientific and logistic problems of dealing with genetically diverse material growing on variable sites; moreover, trees generally do not start to flower until a large and complex shoot system has been built up, and even then flowering is often sporadic (Plate 15).

At present, forest trees are usually grown from seeds collected (i) in those parts of the natural range (provenances) of a species which appear most promising, or (ii) from thriving local plantations or smaller groups of trees. Only in a minority of instances has it been possible to harvest large, regular crops of seed from selected and tested parent trees, because the breeding of improved strains is in its infancy. This is certainly not due to a lack of genetic diversity, but rather because of the twin constraints of uncertainty as to what causes tree variation, and inability to stimulate heavy flowering in the chosen parents.

Two developments during the last 10 years or so have greatly increased the chances of more rapid tree improvement, besides having other potential effects on forestry and arboriculture. They are:

1. The rapid development of techniques for rooting cuttings taken from young trees (Hinds & Krugman, 1974; Bowen *et al.*, 1977; Eliasson, 1977), so allowing the production of clones of genetically 'identical' plants. It now seems likely that this may prove feasible for most of the world's commercial timber species, as well as for many fruit, shelter and ornamental trees. The implications of easy vegetative regeneration are far-reaching for genetical, silvicultural and other research, and also for temperate and tropical plantation practice.

2. Our increasing ability to stimulate male and female flowers at will in some species (Pharis & Kuo, 1977; Longman, 1975, 1978). For example, by treating *Thuja plicata* with the plant hormone gibberellic acid (GA_3), male and female cones can be obtained in all genotypes so far tested. They were produced, depending on sites and rates of application in small and large quantities on (i) large and small trees, (ii) whole and individual branches and (iii) "juvenile" and "mature" cuttings. In species reacting in this way to GA_3, the bulk production of quality seed from selected parents, and the breeding of improved strains and hybrids, can now go ahead on an annual programme. But for most other trees our knowledge of the control of sexual reproduction is deficient. However, in these instances other techniques, including bark-ringing, may prove to be of wide applicability.

Besides their immediate practical importance, these advances enable the examination of several difficult aspects of plant physiology from a fresh standpoint. Because small potted plants can now be used, the factors influencing the formation of flower initials may be studied experimentally in controlled environments. Micro-injection systems allow hormone solutions to be applied with a degree of precision, enabling the differences between male- and female-bearing shoots, and between juvenile and mature tissues, to be investigated (Longman, 1976). The effects of other growth substances can also be more readily determined against a background of flower initiation induced by gibberellin treatments than is the case when relying on sporadic natural initiation.

1. Some environmental factors influencing floral initiation

As plant physiologists now recognise, the change from a vegetative to a reproductive shoot apex is probably governed by a balance of hormones, inhibitors and other substances, the concentrations of which are presumably modified by changes of environment (see Krekule, 1979). Even in the commonly studied herbs, flowering appears to be evoked by specific combinations of external and internal conditions, and probably involves more than one step. In more complex structured forest trees, it is therefore not surprising to find that flower formation is influenced by many factors.

Photoperiod has been known for nearly 50 years to influence flowering in a few woody shrubs (Allard, 1935), as well as large numbers of herbaceous species. However, substantive experimental evidence for forest trees has only been produced during the last decade or so. For example, by rooting cuttings

from specimens of *Pinus contorta* with a strong propensity for reproductive activity, clones have been identified which can form male and female cones freely from the stage when the plant is only 10-20 cm tall. When grown in short days (10 h), such trees formed 6 times as many female cones as were initiated in long days (19½ hr), both sets of plants having received the same daily amounts of light energy (Figure 45). Interestingly, *P. contorta* clone 8996 regularly tends to produce a preponderance of female cones, whereas clone 8997, from the same provenance, is more strongly male (see Figure 46).

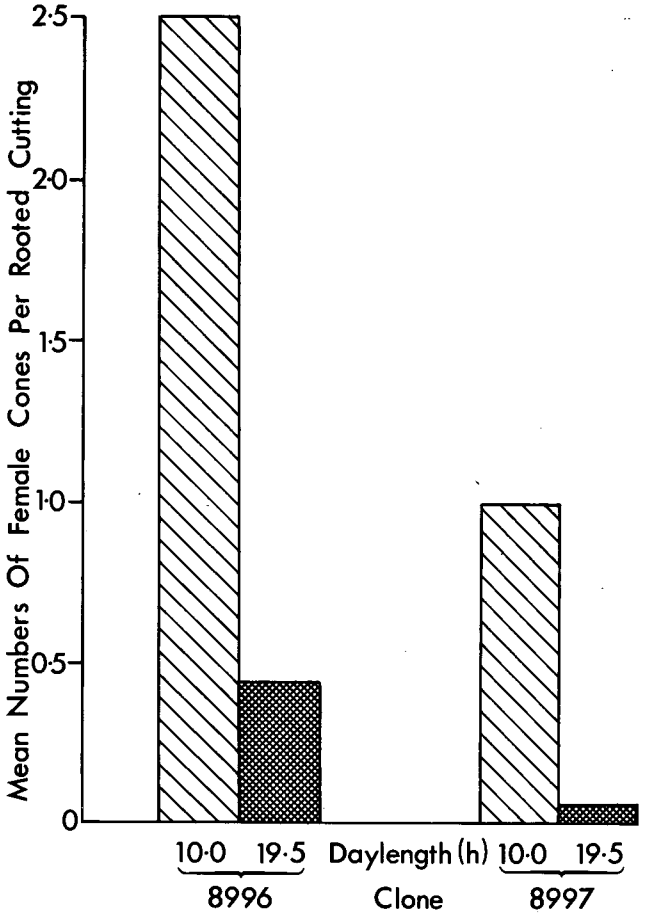

Fig. 45 *Mean effects of short (10 hr) and long (19½ hr) days on the production of female cones by cuttings of 2 clones (8996 and 8997) of lodgepole pine* (Pinus contorta). *Numbers of female cones per plant initiated in controlled environment cabinets, averaging over 2 temperatures and 2 hormone treatments.*

Unlike the situation in *P. contorta,* flower formation in *Thuja plicata* and *Cupressus arizonica* is favoured by long days (Pharis *et al.,* 1969). Using plants treated with GA_3, it is possible to show that male and female initiation commences freely in long days, but the proper development of cones is dependent on a period of short days.

Temperature also influences floral initiation in *T. plicata,* warmer temperatures interacting positively with long days during early initiation, and cooler conditions promoting subsequent cone development. A stimulating effect of warm temperatures during the critical first stage of flower initiation might perhaps explain, at least in part, the many reports of heavy flowering in other species of forest trees in fine summers, or when branches or whole plants are grown under polythene. However, when other factors cannot be excluded, it is unwise to make unwarranted generalisations. Indeed, in the *P. contorta* experiment described above there was apparently little or no effect of temperature on female cone formation, while male cones were significantly more frequent in cool conditions (Figure 46). Perhaps temperature will be found, in due course, to have a range of effects depending on specific day and night regimes, or on light intensities before, or during, experimental treatments.

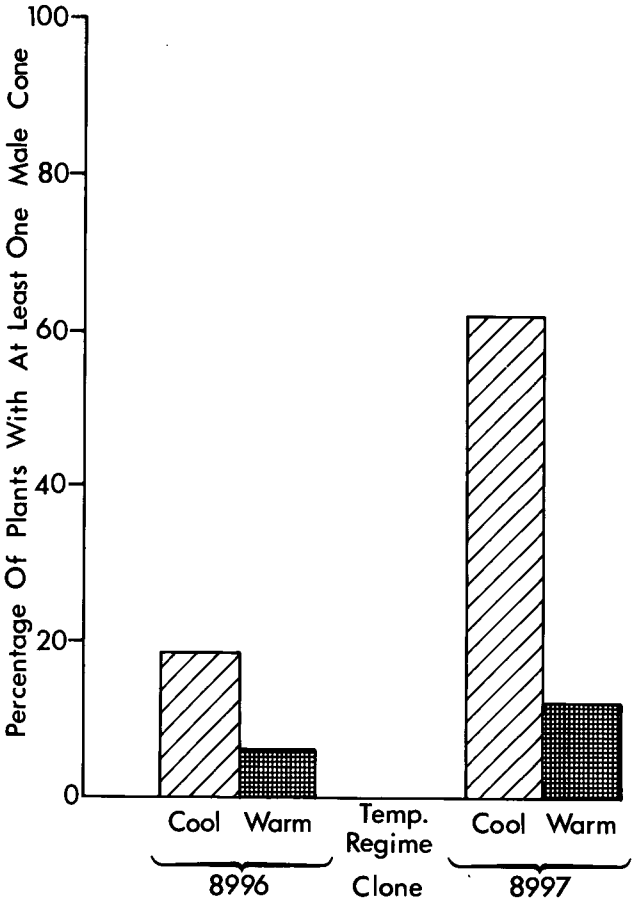

Fig. 46 *Mean effects of temperature on the proportion of trees initiating male cones by cuttings of 2 cones (8996 and 8997) of lodgepole pine* (Pinus contorta). *Temperature regimes: cool - 15°C day/ 8°C night; warm - 22°C day/15°C night.*

2. Developing practical techniques for flower induction

As already mentioned, intense cone formation can be reliably stimulated by GA_3, but this effect seems to be confined to trees in the Cupressaceae and Taxodiaceae. In *T. plicata,* for instance, seed yields of up to 45 kg ha^{-1} have been obtained by injecting selected parent trees, 15 years old growing in a seed orchard, with 50 mg GA_3, in June of the previous year (Longman, 1978). In small potted plants, male and female coning has been stimulated in selected clones of *Cupressus macrocarpa* (Monterey cypress) and *Chamaecyparis nootkatensis* (Nootka cypress). By adjusting the date of injection with GA_3, the flowering of the 2 species has been synchronised, enabling crosses to be made. In an experiment done in a glasshouse in west Wales with the help of Mr H. Ovens, it is hoped that the many ripening cones will contain viable seed of new forms of X. *Cupressocyparis leylandii,* the valuable but sterile leyland cypress of which only 10 clones exist (Ovens *et al.,* 1964).

Using combinations of genetical selection, environmental control and hormone injection, it is clearly becoming easier for the physiologist to help the tree-breeder to (i) re-synthesize hybrids which originated from a narrow and not necessarily superior genetic base, (ii) attempt a range of new crosses including the transfer of specific desirable attributes. Furthermore, these gains could subsequently be evaluated or exploited by vegetative propagation.

In broadleaved trees, as with the Pinaceae, bark-ringing at present offers the most likely method of increasing the incidence of flowering (Longman, 1978). For instance, the removal of complete rings of bark about midway up the main stems of clonal plants of 2 provenances of *Betula pendula* greatly stimulated the formation of female catkins in years 1 and 2, and of male catkins in year 2 (Figure 47). The technique has also been used successfully in the field where, instead of mainstems, branches on larger specimens of several forest tree species can be treated, the effects being restricted to the parts distal to the zones of ringing. Similar responses were achieved by ringing 2 year old birch seedlings, indicating that the time from germination to first flowering can be substantially shortened in this genus. In the absence of bark-ringing, birch seedlings can be stimulated to flower early by continous growth in long days (Longman & Wareing, 1959), and crossing is now being achieved on a 2-year, or even a 1-year cycle in large polythene houses (Lepisto, 1973; Karki, pers. comm.).

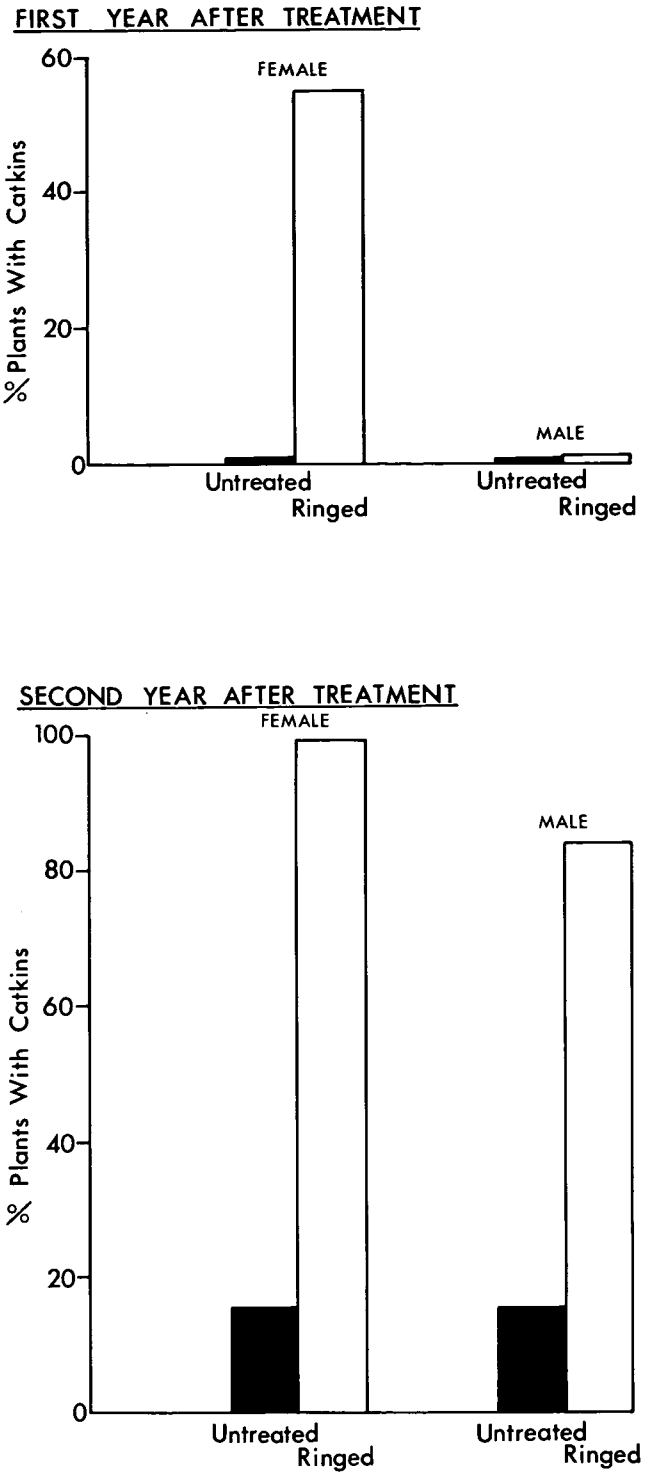

Fig. 47 *Effects of ringing mainstems of* Betula pendula *cuttings, grown in cool glasshouse conditions, on the production of female and male catkins in the first and second years after treatment.*

Perhaps the most important tasks in tree improvement during the coming decades will be the development and evaluation of strains of forest trees with better form and a greater tolerance of pests, pathogens and environmental extremes. To facilitate their production, testing and use, it is necessary to widen our knowledge of reproductive physiology to a more diverse array of species, native as well as introduced.

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24. PHYSIOLOGICAL APPROACHES TO THE CONSERVATION AND IMPROVEMENT OF *TRIPLOCHITON SCLEROXYLON*–A WEST AFRICAN TIMBER TREE

R.R.B. LEAKEY

Triplochiton scleroxylon K. Schum. is an important timber tree of West Africa (Plate 16), whose genetic resources have been severely depleted by the clearance of high forest for: (i) usable timber, (ii) the needs of shifting agriculture, and (iii) the construction of roads, towns, etc. Although a pioneer species, natural regeneration of *T. scleroxylon* is spasmodic because in most years few seeds are produced. Even when flowering is prolific, many fruits are destroyed by pests and pathogens, eg *Apion* and *Mycosyrinx* spp (Jones, 1975*b*). In addition, seeds remain viable for only a few months (Bowen & Jones, 1975), so restricting the possibilities of commercial plantings.

In 1970, the UK Ministry of Overseas Development established 2 projects on *T. scleroxylon*, jointly aimed at the conservation and improvement of this species. One is based at the Forestry Research Institute of Nigeria (FRIN) and the other at ITE Edinburgh. The former is primarily concerned with (i) the natural distribution and phenology of *T. scleroxylon* in West Africa (Jones, 1975*a*), (ii) the collection of seed and establishment of a gene bank, (iii) fruit maturation and factors affecting seed storage (Jones, 1976; Bowen & Jones, 1975; Howland & Bowen, 1977), (iv) techniques for vegetative propagation (Howland, 1975*a, b, c*) to provide alternative planting stock and (v) field growth of clonal plantations (Howland *et al.*, 1977). While colleagues in Nigeria have been focussing on these more immediately practical aspects, the ITE team has investigated the fundamentals of some of the physiological mechanisms controlling (i) root initiation in cuttings, (ii) apical dominance and the control of branching, which is of importance to the maintenance of stockplants and the early selection of superior clones, and (iii) flower initiation and seed production, vital to a breeding programme. In this way it is hoped that the overall programme, pure and applied, is properly balanced and may be regarded as a model for the conservation and improvement of other potentially important tropical tree species.

1. Vegetative propagation

Having evolved conditions favouring the rooting of *T. scleroxylon* cuttings in tropicalised glasshouses in Edinburgh (Leakey *et al.*, 1975) 2 aspects have been studied in detail:

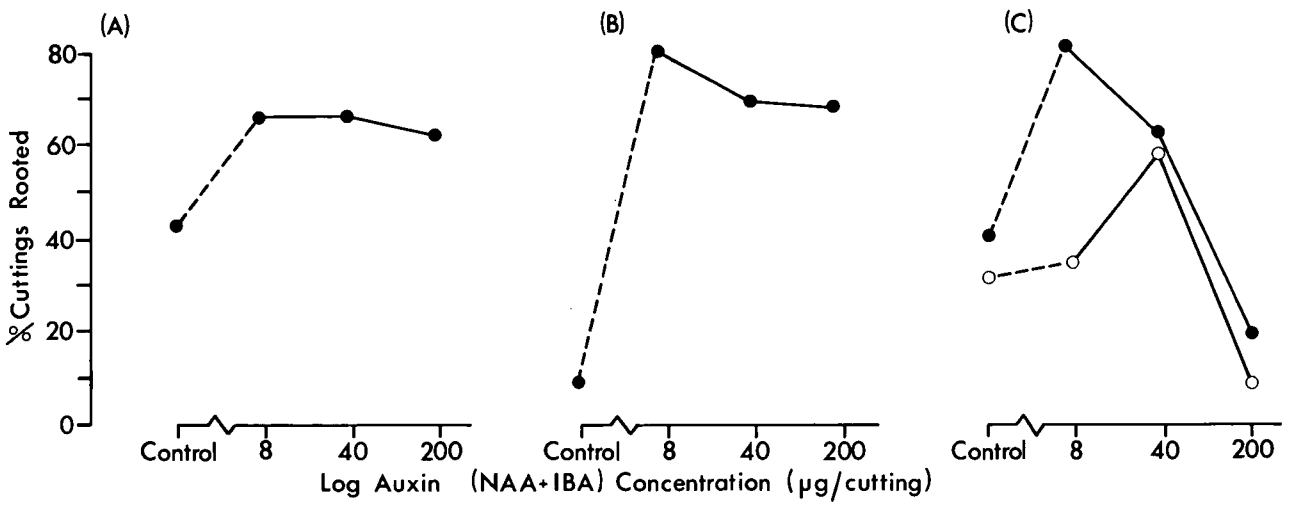


Fig. 48 *Effects of different concentrations of a 50:50 mixture of NAA and IBA (auxins) on the rooting of leafy single-node cuttings of* T. scleroxylon.

(A) An easily propagated clone, relatively insensitive to different auxin concentrations

(B) Clone whose rooting is considerably enhanced by a wide range of auxin concentrations

(C) Two different clones (● and ○) requiring specific auxin applications with different optimum concentrations.

1.1 Inherent variation in relation to rooting ability and responses to rooting hormones

Howland (1975*b*) found that applications of auxins (NAA—naphthalene acetic acid: IBA, indole-3-butyric acid) were usually unnecessary for rooting. Subsequently, however, it has become apparent that rooting ability varies widely within *T. scleroxylon*. Some clones root well with or without auxins while within a group of poor rooters the responses to auxins may be (a) virtually independent of their concentrations or (b) concentration specific (Figure 48). Clones such as 8021

are more responsive to IBA whereas others (eg 8036) respond similarly to IBA and NAA. For practical purposes, the recommended application for *T. scleroxylon* cuttings is now a 50:50 mixture of NAA & IBA at 40 μg/cutting, or a 'quick-dip' in 0.4% alcoholic solution. This application enhances rooting and increases the number of roots per cutting.

shoots of decapitated stockplants support the hypothesis that competition for a root factor affects their subsequent rooting ability (Figure 49*a*). Furthermore shoots only 5-6 nodes apart had markedly different rooting abilities even when the level of inter-shoot competition was constant (Figure 49*a*). This result, however, can probably be attributed to an effect of light, for, when equally

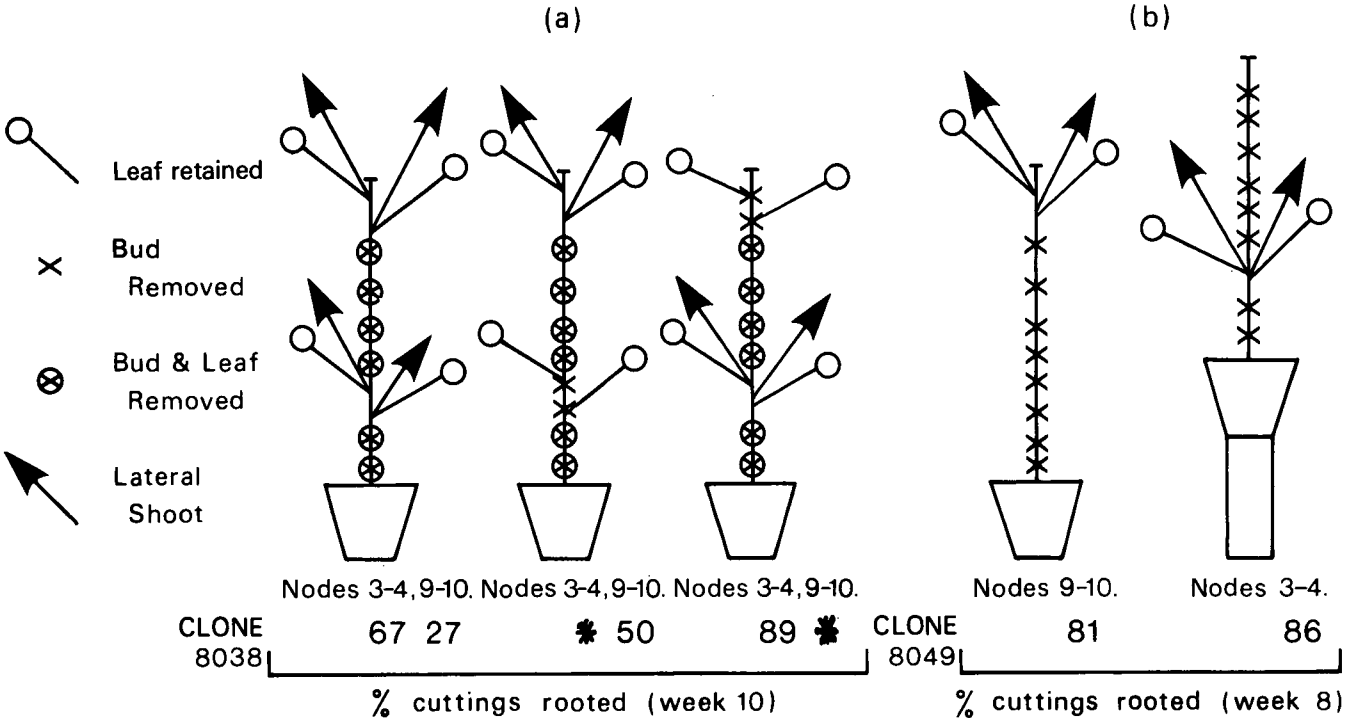


Fig. 49 *Effects of node position and competition between shoots on percentage rooting of leafy single node cuttings of* Triplochiton scleroxylon. **Lateral shoots removed as part of treatment and therefore not available for later rooting.*

1.2 Identification of some stockplant effects on rooting

Cuttings taken from different parts of the same stockplant have different rooting abilities, the overall percentage rooting also reflecting the physiological condition of the stockplants. These effects may be ephemeral or persistent, the latter being generally attributed to 'phase-change', the change from juvenility to maturity, which probably includes many physiological processes. Experiments with *T. scleroxylon* have tested the effects of stockplant orientation, soil nutrient status, stockplant size, numbers of shoots/plants, position of shoots on mainstems and the removal of stem apices from stockplants. In all these experiments, cuttings from basal shoots were always the easiest to root. Nonetheless, the degree of success was dependent upon the supply of soil nutrients and the degree of competition for a gravity sensitive factor, originating in stockplant roots, which stimulates root initiation in cuttings. The rooting success of cuttings was inversely proportional to the number of shoots per stockplant. Experiments which limited growth to particular lateral illuminated, rooting percentages of cuttings from apical and basal shoots were similar (Figure 49*b*).

TABLE 33 Effects of different day lengths on the growth of vegetatively propagated plants of *Cordia alliodora* of mainstem and lateral shoot origin, after 5 weeks.

	Origin of cuttings			
	Plant height (mm)		Leaf area (cm^2)	
	Mainstem	Lateral	Mainstem	Lateral
Long days (15 h)	326	205	1078	740
Short days (10 h)	126	89	673	415

All these factors are therefore contributing to short-term carry-over or 'c' effects unrelated to persistent phase-change, but of considerable importance to the development of stockplant management systems aimed at the production of uniform planting stock. The degree of undesirable traits such as plagiotropism (Plate 17) and reduced vigour (Table 33) incorporated in cuttings established from badly-managed stockplants requires further investigation.

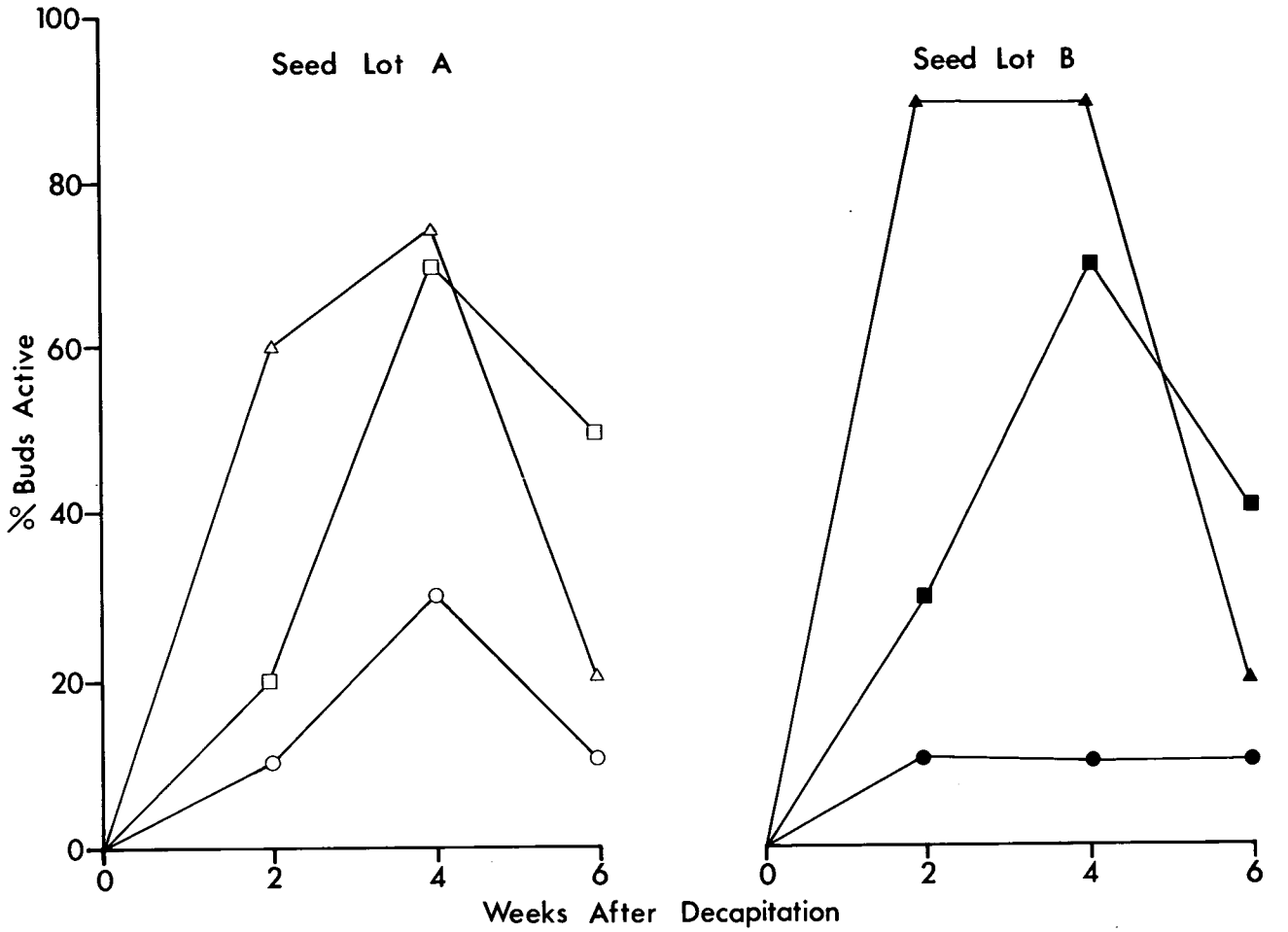


Fig. 50 *Genetic variation in bud growth of* T. scleroxylon *seedlings following decapitation at node 10, 4 months from germination (3 seedlings per seed lot* △, □ *and* ○; ▲, ■ *and* ●*).*

2. Clonal selection

Forest plantings of clones derived from seed collected from the entire natural range of *T. scleroxylon,* from Zaire in the east to Sierra Leone in the west, have been made by colleagues in Nigeria. Meanwhile attempts have been made in Edinburgh to develop a rapid test for predicting branching habit of mature trees, the test being based on the way in which lateral shoots develop after the removal of the dominating mainstem apex. In the event it was found that the responses of seedlings from the same mother tree differed greatly—in some, apical dominance was quickly re-established with relatively few buds becoming active whereas in others with weak apical dominance many buds flushed, at least temporarily (Figure 50). These differences were subsequently shown to be inherent.

Apical dominance is affected by many environmental and physiological variables which need to be standardized for predictive tests. These include:

2.1 Numbers of leaves per plant and their positions

Fewer lateral shoots extended on undefoliated plants than on those whose leaves were either partially or fully removed (Table 34);

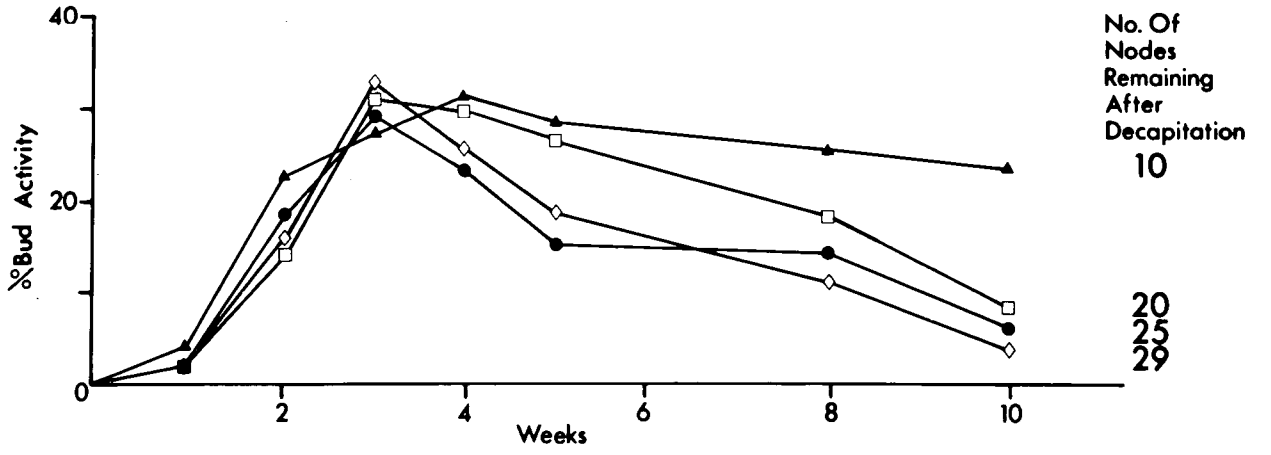
TABLE 34 Effects of partial and complete defoliation on the activity (%) of buds remaining when the 2 uppermost nodes were removed from *T. scleroxylon* plants.

	Weeks after removing uppermost nodes		
	1	5	8.5
Undefoliated	50.0	22.3	13.9
Top 5 nodes defoliated	61.7	32.3	17.4
Nodes 6-10 defoliated	78.5	31.1	22.0
Totally defoliated	62.5	32.8	26.0

2.2 The amount of stem removed when decapitating

When different amounts of stem were cut from a uniform batch of trees, the percentage of buds

(a) Plants of uniform height cut to different numbers of nodes.



(b) Terminal bud and uppermost node removed from plants of different sizes.

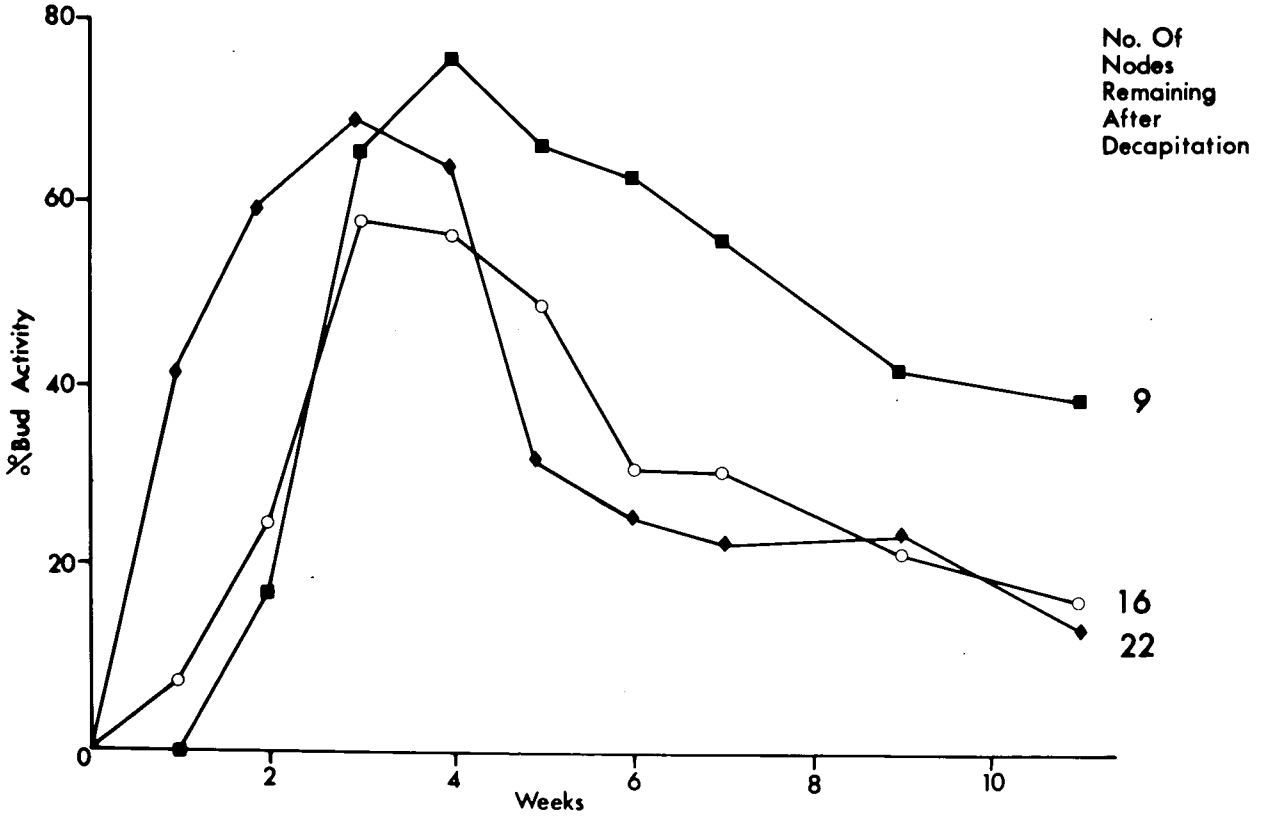


Fig. 51 *Effects of decapitation at different heights on bud activity in* T. scleroxylon.

which became active did not vary appreciably (Figure 51*a*). On the other hand when plants of different heights were cut to the same level the percentages of active buds were more variable (Figure 51*b*).

2.3 Nutrient status

Although other species can be released from apical dominance by the application of fertilisers (McIntyre, 1977), effects on bud activity of decapitated plants of *T. scleroxylon* have not been clearly demonstrated. Numbers of lateral buds flushing after the removal of apical meristems seemed to be independent of nutrient status but subsequently dominance was asserted sooner in plants with fewer nutrients.

It should soon be possible to calibrate results from such predictive tests with clones planted in Nigeria.

3. Flowering and flower induction

In nature, *T. scleroxylon* rarely flowers before it is 15-20 years old, when, because of its size, controlled pollination is already almost impossible. Grafts and cuttings from mature trees have flowered in the forest nursery in Nigeria, and controlled pollinations resulted in the production of viable seed. Cuttings from mature trees have flowered and fruited in tropicalised glasshouses in Edinburgh, but more importantly 12 young trees, of 2-3 years old, have also flowered. Seeds from self-pollinations did not germinate, whereas those from controlled cross-pollinations did. Stocks of these clones with a propensity to flower are being increased so as to make a thorough examination of flower induction, recognising that the techniques used on temperate trees (Longman, 1975) may be inappropriate.

4. Conclusion

To date, many aspects of vegetative propagation and some of flower induction have been investigated for *T. scleroxylon*. There is now some hope that this species will be sustained and that supplies of its timber 'Obeche' will be safeguarded. Already extensive experimental plantings have been made. Improvement by the combination of sexual and asexual propagation (Longman, 1976; Bowen *et al.*, 1977; Longman *et al.*, 1979) requires that the key to flower induction in young trees be found yielding progeny which would contribute both to the gene bank and to commercial forestry. Such an approach could also benefit many other 'endangered' tropical tree species.

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The fauna, including pests, of woodlands and forests

25. INSECTS ON EXOTIC BROADLEAVED TREES OF THE FAGACEAE, NAMELY *QUERCUS BOREALIS* AND SPECIES OF *NOTHOFAGUS*

R.C. WELCH

Since the early 1970s, and following a number of earlier plantings, it seems that American red oak *(Quercus borealis* syn. *Q. rubra)* has been used more widely in "amenity plantings". This species has been included with other *Quercus* spp in commercial forestry returns giving details of areas planted.

Conservationists regularly quote Southwood (1961) in crediting native oaks as having more insect species associated with them than other British trees. Thus, if red oak was to become widely planted, would the species become an alternative food source for the many insects which depend on the English oaks? Earlier enquiries showed that virtually nothing was known about insects colonizing *Q. borealis* in Britain.

From studies in North America, it was known that some Lepidoptera larvae such as *Operophtera brummata* (winter moth) killed red oaks by repeated defoliation (Embree, 1967). Because this pest species also occurs in Britain, it might similarly jeopardize *Q. borealis* here. Moeller (1967) suggested that the general immunity of *Q. borealis* to insect attack in Germany was due to its planting in mixtures with other *Quercus* spp. However, its defoliation by *Tortrix viridana* (green oak-roller) was observed in a relatively pure stand of 743 hectares. More recently, Zlatanov (1971) published an account of insect pests on 7 species of oak in Bulgaria, including *Q. rubra* (Table 35), although his lists include many pests not known to occur in Britain. Five of Zlatanov's 7 wood-boring pests of *Q. rubra* are "British" species, as are all but one of the leaf-feeding Lepidoptera. However, 16 species of the latter group occur only "rarely" or "to a lesser extent" on *Q. rubra.* Two of the root-feeding pests occur in Britain.

TABLE 35 Insect pests of 3 *Quercus* species in Bulgaria (after Zlatanov 1971).

A. Insect species by orders	*Q. robur*	*Q. cerris*	*Q. rubra*
Coleoptera	45	40	14
Lepidoptera	67	49	29
Hymenoptera	40	15	3
Homoptera	14	8	6
Diptera	2	4	–
B. Insect species by damage type			
Wood borers	41	34	7
Leaf feeders	65	49	28
Gall formers	39	15	3
Pests of current year's growth	13	7	6
Root feeders	8	8	7
Pests of flowers and fruits	3	3	1

With the help of the Forestry Commission, foliage samples were taken in 1972 of *Q. borealis* (P. 1950) and *Q. robur* (P. 1950) growing in Bramfield Forest, Hertfordshire. Diptera, mostly 'casuals' using foliage for temporary shelter, were equally distributed on *Q. robur* and *Q. borealis,* whereas larval Lepidoptera were 3 times more numerous on *Q. borealis* than on *Q. robur.* Otherwise, the differing groups of insects were more numerous on *Q. robur* than on *Q. borealis* (Table 36). Whereas 798 Hymenoptera of the gall-forming Cynipidae were found on *Q. robur,* none were detected on *Q. borealis.* Zlatanov listed 3 species of Cynipidae on *Q. rubra,* all of which occur in Britain, and 2, *Neuroterus numismalis* (silk button spangle gall)

TABLE 36 Numbers and types of insects found on foliage of *Quercus robur* and *Q. borealis* sampled from Bramfield, Herts., between May and October 1972*.

	Q. robur	*Q. borealis*
Lepidoptera (larvae)	98	319
Lepidoptera (adults)	12	8
Coleoptera	99	61
Homoptera (Aphidae)	99	12
Homoptera (Others)	14	9
Heteroptera	9	1
Psocoptera	56	7
Hymenoptera	78	22
Hymenoptera (Cynipidae galls)	798	–
Diptera	84	80
Dermaptera	6	2
Araneae	144	30
Opiliones	8	2

and *N. quercus-baccarum* (common spangle gall), were present on *Q. robur* at Bramfield. Interestingly, the weevil *Curculio pyrrhoceras,* whose larvae are parasites or inquilines in the galls of *N. quercus-baccarum* (Morris, 1976), were only found on *Q. robur* (Table 37). Of the Coleoptera, specimens of *Phyllobius argentatus* were detected with equal frequency on the 2 species of *Quercus,* whereas *Polydrusus cervinus* was commoner on *Q. robur* than *Q. borealis,* a difficult differential distribution to explain, remembering that the adults of both species are general leaf feeders while their larvae consume roots (Table 37). Single specimens of *Coeliodes dryados,* whose larvae are thought to feed in oak buds, were found on both oaks (Morris, 1976). Two species of *Rhynchaenus* (blotch mining weevils), although collected in very small numbers, were restricted to *Q. robur.* More ladybirds, *Adalia 10-punctata,* were found on *Q. borealis.* From these preliminary investigations, it seems that some insects, notably the Cynipidae colonizing *Q. robur,* were not attracted to *Q. borealis.* Following a survey made in Nova Scotia by Brookfield (1972), it was found that the Nearctic species of Cynipidae from *Q. borealis* failed to stimulate gall formation on *Q. robur.* During 1973, more Forestry Commission plantings in East Anglia were examined, in addition to

TABLE 37 Occurrence of selected Coleoptera on foliage of *Quercus robur* and *Q. borealis* sampled at Bramfield, Herts., between May and October 1972*.

	Q. robur	*Q. borealis*
Rhagonycha lignosa (Muell.)	6*	30
Malthodes marginatus (Lat.)	5	–
Adalia 10-punctata (L.)	2	10
Stilbus testaceus (Pz.)	5	–
Cortinicara gibbosa (Hbst.)	20	3
Phyllobius argentatus (L.)	6	6
Polydrusus cervinus (L.)	18	1
Strophosomus melanogrammus (Forst.)	3	3
Coeliodes dryados (Gmel.)	1	1
Curculio pyrrhoceras Marsh.	11	–
Rhynchaenus avellanae (Don.)	3	–
Rhynchaenus quercus (L.)	1	–

* total numbers in 12 samples on each of 8 dates

TABLE 38 Relative abundance in June 1978 of selected Coleoptera on exotic species of *Nothofagus* and *Quercus* grown at Thetford Forest.

	Quercus borealis	*Nothofagus obliqua*	*Nothofagus procera*
Dalopius marginatus (L.)	7	4	1
Denticollis linearis (L.)	–	2	–
Cantharis decipiens Baudi	1	1	–
Cantharis nigricans (Muell.)	1	–	–
Rhagonycha lignosa (Muell.)	6	2	5
Dryophilus pusillus (Gyll.)	14	12	31 c
Brachypterus urticae (F.)	1	–	–
Scymnus suturalis Thnb.	–	–	2 c
Exochomus 4-pustulatus (L.)	3 + 1 c	–	–
Aphidecta obliterata (L.)	–	2	3 c
Adalia bipunctata (L.)	1	–	–
Coccinella 7-punctata L.	2	6 + 3	3 + 3
Anatis ocellata (L.)	–	3	4 c
Calvia 14-guttata (L.)	–	–	2
Enicmus transversus (Ol.)	–	–	1
Cortinicara gibbosa (Hbst.)	–	–	1
Rhinosimus planirostris (F.)	1	1	–
Anaspis rufilabris (Gyll.)	1	–	1
Deporaus betulae (L.)	–	1	–
Otiorhynchus rugostriatus (Goez.)	1	2	–
Phyllobius argentatus (L.)	18	37	50
Polydrusus cervinus (L.)	1	–	–
Strophosomus capitatus (De G.)	5	7	17
Strophosomus melanogrammus (Forst.)	5	–	1
Rhynchaenus quercus (L.)	1	–	–

c = spp associated with conifers.

+1 = plus one larva.

mature specimens of *Q. borealis* in the grounds of stately homes in southern England. Despite a wide variety of Coleoptera on decaying timber and associated fungal fruiting bodies, no cynipid galls were discovered.

When studying the fauna of introduced plant species, there is always the possibility of discovering something unusual. Aphids from *Q. borealis* were sent to Dr H.L.G. Stroyan who identified 9 specimens of *Tuberculoides borealis,* a hitherto undetected British species, which had only been described in 1971. Subsequently, Dr Stroyan identified this aphid from *Q. robur* (Stroyan, 1977).

Experience with *Q. borealis* has demonstrated that exotic species of a genus well represented in Britain and Europe may be "unacceptable" to some elements of our native insect fauna. Such a condition would be expected to be even more pronounced among species of *Nothofagus,* an exotic genus of the Fagaceae, with its origins in the remote temperate zones of South America and Australasia. Although *N. procera* and *N. obliqua* were introduced into Britain much earlier (Nimmo, 1971), importation of seed from Chile in 1954 led to a series of widely distributed small trial plots in 1955 and 1956. Further substantial supplies of Chilean seed have recently become available, and these 2 species are now being widely grown by nurserymen. It is thus likely that these fast-growing hardwoods may become common plantation species in the near future. For this reason, during the summer of 1978, insects were sampled on *N. obliqua* and *N. procera* planted in Thetford and Alton Forests between 1953 and 1959. Insects, dislodged from foliage when beaten, were collected on a square canvas tray 1 m^2

TABLE 39 Species of defoliating Lepidoptera larvae found on foliage of *Nothofagus* spp.

	Nothofagus obliqua	*Nothofagus precera*	*Nothofagus hybrida*
Carcina quercana (F.)	+	–	–
Pandemis corylana (F.)	+	–	–
Pandemis heparana (D. & S)	+	–	–
Epirrata autumnata (Bork.)	–	–	+
Operophtera brumata (L.)	–	+++	+
Ennomos erosaria (D. & S.)	–	+	–
Crocallis elinguaria (L.)	+	–	–
Apocheima hispidaria (D. & S.)	+	–	–
Apocheima pilosaria (D. & S.)	+	+	–
Biston betularia (L.)	+	–	–
Biston startaria (Hufn.)	+	–	–
Agriopis aurantiaria (Hub.)	+	+	–
Agriopis marginaria (Fab.)	+	+	–
Errannis defoliaria (Clerck)	+	++	–
Ectropis bistortata (Goeze)	+	–	–
**Phalera bucephala* (L.)	–	+	–
Orgyia antiqua (L.)	+	–	–
Euproctis similis (Fues.)	+	–	–
Lymantria monacha (L.)	+	–	–
Eilema deplana (Esper)	+	–	–
Orthosia cruda (D. & S.)	–	+	–
Orthosia gothica (L.)	+	+	–
Orthosia stabilis (D. & S.)	+	+	–
Brachionycha sphinx (Hufn.)	+	+	–
Acronicta psi (L.)	+	–	–
Colocasia coryli (L.)	+	+	–

+/++/+++ species recorded from 1, 2 or 3 localities.

* Recorded 1975/76. All others 1978, combined records of R.C. Welch, J.N. Greatorex-Davies and R.M. Brown.

before being counted and identified. However, because numbers of samples were not standardised, the abundance of Coleoptera should only be considered in relative terms (Table 38). Although only 60% of the more numerous species are listed, they illustrate the difficulties of interpretation. The presence of the second most abundant species, *Dryophilus pusillus* (Anobiidae), was more a reflection of site than of the attractiveness of *Nothofagus* spp. This species was most probably associated with *Larix* beneath which *Nothofagus* had been planted. Two other specimens were collected at a second site at Thetford and none were found at Alton. Four of the 7 species of Coccinellidae found on *Nothofagus* spp are similarly associated with conifers. More *Phyllobius argentatus* were found on *N. procera* than on *N. obliqua* at one site, but, at other locations, both species of *Nothofagus* were colonized to the same extent. Most Coleoptera species were poorly represented, the few individuals trapped probably being "accidentals", such as *Brachypterus urticae* which feeds on nettles.

At present, the scant available evidence suggests that very few of the Coleoptera recorded on *Nothofagus* spp are potential pests, but this is not so when considering the Lepidoptera. It is likely that the 26 species so far identified are leaf-feeders to a greater or lesser extent (Table 39). Some of these larvae have been recorded from as many as 12 alternate hosts (Table 40). Interestingly, all but 2 have been observed feeding on native *Quercus* spp, 9 on native *Fagus* and one on *Castanea*, a naturalized alien, all 3 tree genera, like *Nothofagus*, being part of the Fagaceae. In interpreting the results of surveys, note should be taken of the

TABLE 40 Alternate host plants of 26 species of Lepidoptera larvae known to defoliate *Nothofagus* spp.*

Alternate Hosts	Nos. of spp. feeding on:— Family	Genus
FAGACEAE	24	
Quercus		24
Fagus		9
Castanea		1
BETULACEAE	24	
Betula		21
Corylus		9
Carpinus		7
Alnus		7
ROSACEAE	22	
Crataegus		18
Prunus		17
Malus		9
Rosa		6
Pyrus		4
Sorbus		1
Rubus		1
SALICACEAE	17	
Salix		17
Populus		6
TILIACEAE	11	
Tilia		
ULMACEAE	10	
Ulmus		
CAPRIFOLIACEAE	5	
Viburnum		2
Lonicera		3
OLEACEAE	3	
Fraxinus		2
Ligustrum		1
TAXACEAE	2	
Taxus		
PINACEA	2	
Pinus		2
Picea		1
Larix		1
ACERACEAE	1	
Acer		
PLATANACEAE	1	
Platanus		
HIPPOCASTANACEAE	1	
Aesculus		
"Non-tree" families	9	

* of Table 40

occurrence of members of the Rosaceae which are often alternate hosts of polyphagous Lepidoptera.

When planting exotic species of trees, foresters should be aware of potential insect pests, conservationists should know how many insect species they are likely to support, whilst the ecologists may wish to understand the factors determining which insects successfully colonize trees and which do not. Plans have been made with R.M. Brown of the Forestry Commission to sample *Nothofagus* more extensively.

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26. THE SUBCORTICAL FAUNA OF OAK; SCOLYTID BEETLES AS POTENTIAL VECTORS OF OAK WILT DISEASE

M.G. YATES

By now, the havoc wrought by Dutch elm disease, caused by the fungus *Ceratocystis ulmi,* is obvious to us all. Although it can spread locally from tree to tree through root grafts, dissemination over longer distances depends upon the bark-beetles, *Scolytus scolytus* and *S. multistriatus* in the UK We are becoming increasingly aware of another threat, this time to our native oaks. At present oak wilt disease, whose casual fungus *Ceratocystis fagacearum* is also transmitted by bark-beetles, is restricted to N America. To minimise its chances of being introduced into the UK, legislation prohibiting the importation from North America of live oak, oak bark and oak timber with bark attached has been enacted—the first line of defence.

In the United States, *C. fagacearum,* like *C. ulmi,* can be transmitted through root grafts. For its dispersal over longer distances it is dependent upon scolytid beetles of the genus *Pseudopityophthorus* which is not represented in the UK. Nevertheless it is suspected that the UK native oak bark-beetle *S. intricatus* might prove to be an effective vector should *C. fagacearum* be introduced to the UK. For this reason, studies are being made of the biology and ecology of *S. intricatus,* and other scolytids of oak, to assess their potential as oak wilt vectors and to provide a basis for their control if the need arose. Observations have been made on *S. intricatus* breeding in oak logs in Monks Wood National Nature Reserve in the expectation of more intensive studies being made in oak woodland in the New Forest (Plate 18).

The biology and ecology of *S. intricatus* is being analysed against 2 sets of criteria: (i) the potential suitability of *S. intricatus* as a vector of *C. fagacearum,* and (ii) its population dynamics.

1. Suitability of *S. intricatus* as an insect vector of *Ceratocystis fagacearum*

If *S. intricatus* is to be a vector it must:

(i) regularly visit diseased trees,

(ii) leave diseased trees carrying propagules, spores or mycelial fragments of *C. fagacearum,*

(iii) visit healthy oaks in conditions enabling inoculation and successful infection.

The evidence suggests that *S. intricatus* is likely to fulfil the first criterion as it breeds in the bark of dead oaks, and there is little reason to doubt that wilt-killed oaks will provide breeding sites. Branches cut from healthy oaks *(Quercus robur)* and logged during coppicing operations in Monks Wood during spring 1977 proved to be suitable breeding sites for *S. intricatus* which infested the logs during summer 1977 and produced a new generation of adult beetles in the following June. Other oak logs, cut in February 1978, were infested in July and August 1978, but logs first attacked in 1977 were not reinfested during 1978, a series of observations suggesting that oak is suitable for oviposition and breeding only for periods of 12-18 months after death. From North America it seems that *C. fagacearum* competes poorly against saprophytic fungi after killing its host. This being so, beetles attacking oak soon after being killed by *C. fagacearum* are more likely to give rise to emerging beetles contaminated with propagules of *C. fagacearum* than later colonizers. In some respects *S. intricatus* might be a more effective vector than *Pseudopityophthorus* spp. In North America the latter breeds only in small diameter branches (up to 10 cm) which are rarely colonized by *C. fagacearum,* whereas at Monks Wood *S. intricatus* seems to favour thicker branches 10-40 cm diameter which, from American experience, would also be more readily colonized by *C. fagacearum.*

During July 1978, when adult *S. intricatus* were emerging from oak logs in Monks Wood, the lower branches of nearby live oaks were regularly examined. It was found that male and female *S. intricatus* feed on twigs, particularly those at the join between the preceding and current seasons' growth, also in leaf axils and bud axils on current growth. This is termed as 'crotch-feeding'. Feeding wounds made in these positions by *Pseudopityophthorus* species are known in N America to facilitate entry and subsequent infection by *C. fagacearum.* Doubtless similar wounds produced by *S. intricatus* would also favour inoculation of *C. fagacearum* (Plate 19).

The seasonality of crotch-feeding is an important factor influencing the transmission of oak wilt. The susceptibility of North American oaks to *C. fagacearum* is seasonally maximal during spring-wood formation in spring and early summer. But, because crotch-feeding by *S. intricatus* reaches its seasonal peak in Britain during late-wood formation, disease incidence may be minimised because the phases of maximal insect feeding and tree susceptibility are unlikely to coincide.

2. Population dynamics of *S. intricatus*

From sequentially sampled oak logs infested with *S. intricatus,* records are being made of endo- and ectoparasitic hymenoptera, parasitic mites, predatory larvae of Dolichipodidae (Diptera), and of

nematodes and fungi parasitising bark-beetle larvae. Subsequently it is hoped to identify, with key-factor analyses, the relative importance of these different agents on the development of successive generations of *S. intricatus.* Additionally, the effects on larval survival of climatic and environmental influences, such as the insulative properties of bark, will be assessed in field and laboratory experiments and in the development of life tables.

For the future, factors affecting the location and aggregation of breeding populations of *S. intricatus* and the dispersal of resulting populations of emerging adults will be investigated. Studies concerning the involvement of host attractants and pheromones are also planned. The effects of threshold temperatures on the flight of adults will be investigated in the field using oak logs as lures, while mark-recapture methods are being considered for field assessments of the extent (distance) of dispersal.

27. TREES AND THE PHYTOPHAGOUS INSECTS DATA BANK

LENA K. WARD and D.F. SPALDING

There is much information in the literature and in unpublished sources on the food-plants of insects and *vice versa,* but these records are widely scattered. To increase the accessibility of this information, a computerised data bank is being assembled using an IBM 370/165 at the University of Cambridge. Records of insects in Britain and their food-plants in Britain or elsewhere are being abstracted from the literature, from the data of expert entomologists and museum collections, and are being processed. They are supported by full references, an indication of whether or not the insect is regarded as a pest, its broad geographical distribution in the British Isles and the part of the plant eaten. Insects and plants are arranged taxonomically using hierarchical codes to phylum, class, order and family taken from standard texts. Within families the arrangement is alphabetical. All names are checked against current check-lists, and the flexible system can accept records at any level from sub-species to phylum. Where appropriate, records of particular relationships are being qualified, eg 'unreliable' data from continental Europe, etc. The data bank also allows for the description of food chains which include parasites and predators, although this has not been fully implemented yet.

At present, the data bank holds information amounting to 7663 insect/food-plant records, and a few hundred insect/insect records. Some of these records are corroborative observations from different sources. There are entries for Heteroptera; Homoptera, Cercopidae, Delphacidae and some Cicadellidae; Hymenoptera, Symphyta and most families of Coleoptera: those for Thysanoptera, Hymenoptera Cynipidae, other families of Homoptera and the remaining Coleoptera will be entered shortly.

Trees generally have more species of insects associated with them than woody shrubs, perennial herbs and other plant groups (Lawton & Schöder, 1978). This is probably because of the more complicated structure of trees. With the introduction of exotic trees and shrubs in forest and amenity plantings, the insect fauna of the UK is being altered by the introduction of associated insects; also the feeding habits of native insects are likely to change with the availability of large plantations of exotic species (Strong *et al.,* 1977; Strong, 1979). It is hoped that the data bank will be a useful tool for collating and updating records in this complex field of work.

As an example of using the data bank, a very preliminary comparison can be made of the fauna of *Pinus,* a genus with a species native to Britain, and *Picea,* which is wholly introduced (Tables 41 & 42). At the generic level for the plants, the data bank records 105 insects for *Pinus* and 80 for *Picea* (at 31.3.1978). These records show that 26% of the species on *Pinus* are specific to that genus, while for *Picea* the corresponding figure is only 4%. The interpretation of this result is speculative until more data are available. However, it is thought that the stenophagous species, incidentally those more likely to be of conservation importance, occur on

TABLE 41 Food-plants of 53 species of phytophagous insect recorded on *Pinus sylvestris* (from the data bank records at 31.3.79)

Most specific	14	Insects restricted to *Pinus sylvestris*
	4	Insects of *P. sylvestris* occurring on other species of *Pinus*
	13	Insects of *P. sylvestris* occurring on *Picea* as well as on *Pinus*
	6	Insects of *P. sylvestris* occurring on a variable range of food-plants in the Pinaceae including *Pinus, Picea, Abies, Larix* and *Pseudotsuga*
	6	Insects of *P. sylvestris* occurring on Cupressaceae as well as on Pinaceae
	1	Insect of *P. sylvestris* occurring on Taxaceae as well as on Pinaceae
Least specific	9	Insects of *P. sylvestris* occurring on angiosperms as well as on gymnosperms

TABLE 42 Food-plants of 31 species of phytophagous insect recorded on *Picea abies*

Most specific	2	Insects restricted to *Picea abies* (NB no insects recorded on *Picea abies* as well as other species of *Picea*)
	7	Insects of *P. abies* occurring also on *Abies* (sub-fam. Abietoideae)
	1	Insect of *P. abies* occurring also on *Pseudotsuga* (Abietoideae)
	12	Insects of *P. abies* occurring on *Pinus* (Pinoideae) as well as on Abietoideae
	6	Insects of *P. abies* occurring on a variable range of food-plants in the Pinaceae, including *Pinus, Abies, Pseudotsuga, Larix* and *Cedrus*
Least specific	3	Insects of *Picea abies* occurring on angiosperms as well as on gymnosperms

Pinus in the relicts of the Caledonian forest. There is naturally no equivalent for *Picea.* Evolutionary relationships within the family Pinaceae could also be involved, for *Pinus* is thought to be monotypic of the sub-family Pinoideae, while *Picea* is in the sub-family Abietoideae together with *Abies, Pseudotsuga* and *Tsuga* (Engler, 1954). A more taxonomically isolated plant genus might be expected to have a more specific fauna. At the species level for the plants, there are data for species of *Pinus* and 2 of *Picea.* Of the phytophagous insects recorded on *P. sylvestris,* 14 species are without alternative hosts, 4 occur on other species of *Pinus* as well as on *P. sylvestris,* while 13 occur also on *Picea.* Nine are polyphagous to the extent that they also feed on Angiosperms. Of the phytophagous insects of *Picea abies,* 2 of the 31 species seem restricted to this host, not even occurring on other species of *Picea* (Table 42). None of the *P. abies* species have yet been recorded feeding on members of the Cupressaceae.

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28. POPULATION STUDIES OF WOODLAND BUTTERFLIES

E. POLLARD

The population ecology of several rare or locally distributed butterflies has been studied in the Institute of Terrestrial Ecology to understand factors determining their abundance and so possibly enable appropriate conservation measures to be taken. Counts of individuals at each stage of the life cycle have been made over several generations, with the subsequent compilation of life tables. Using these data it has been possible to use 'k factor' analyses in attempts to show at which stage or stages major fluctuations in mortality occur which determine fluctuations in numbers of adult butterflies. Although, in the longer term, there may be underlying trends in population size attributable to slow and perhaps imperceptible habitat changes, these trends are likely to be masked, in the relatively short period of a population study, by annual fluctuations related to short term factors such as seasonal differences in weather, or in the abundance of predators or parasites. Nonetheless if 'sensitive' stages are identified, it may be possible to modify the habitat by management, to improve survival and increase the numbers of the species in question.

This paper briefly describes 4 population studies of woodland butterflies and refers to a new scheme for monitoring the abundance of butterflies, specifically designed to identify longer term trends.

1. Population studies

1.1. White admiral *Ladoga camilla* L.

At the beginning of this century the white admiral had a very much more restricted distribution in England than now. It was largely confined to an area centred around the New Forest, but in the 1930s and early 1940s it spread across much of southern England, as far north as Lincolnshire, arriving at Monks Wood during this period. Its larvae feed on honeysuckle, *Lonicera periclymenum* L. The larval stage lasts from late summer of one year to June of the next. At Monks Wood annual fluctuations are largely the result of differences in survival of late instar larvae and pupae in early summer (Pollard, 1979). In cool weather, these stages are protracted and mortality caused by bird predation is high, whereas in warm weather they are of short duration, mortalities are few and hence large numbers of adults emerge. Thus, there is a direct association between temperature and adult numbers, early (and by definition warm) seasons favouring this species. A historical analysis of the spread of the species based on reports in entomological journals, showed that the spread of this butterfly coincided with a period when early summer temperatures were consistently high (Plates 20 and 21).

However, the extended geographical distribution of the white admiral is unlikely to be solely attributable to weather; habitat changes are almost certainly also involved. Its eggs are laid in areas of light shade at the edges of rides or within woodland, usually on old honeysuckle. The adults fly widely and exploit areas of light shade which abound in neglected coppice. In contrast, an actively managed coppice woodland provides virtually no areas of suitable habitat as it changes too quickly from an open stand to dense shade.

Coppice management declined late in the 19th century, the decline continuing until amounts of actively managed coppice are now negligible (eg Peterken, 1976). However, during the warm early summers of the 1930s and 1940s, large areas of neglected coppice seem to have provided ideal conditions for the build up and spread of the white admiral. Subsequently, the white admiral has been lost from many, but not all, of the sites which it colonised in the 1930s and 1940s. However, its conservation in nature reserves is probably not too difficult, provided rides are kept wide to provide some sunny areas. Otherwise, lack of management, especially of old coppice woodland, will in this case ensure that suitable breeding areas are retained. The species may, however, always be at risk in exceptionally cold summers.

1.2 Black hairstreak *Strymonidia pruni* (L.).

This species, one of the rarest British butterflies, was studied by Thomas (1974). It occurs almost exclusively in woods on heavy clay soils in a belt between Oxford and Peterborough; its colonies are localised within woods and sometimes persist for long periods, even up to 50 years. Its larvae feed on blackthorn, *Prunus spinosa* L., typically in glades, rides and at woodland fringes, the clearance of blackthorn for forestry or other purposes accounting for the disappearance of most colonies.

As might be expected of such a tenacious species, it is a poor colonizer. Several times it has been successfully introduced to sites only 5-8 km distant from existing colonies. It can, however, colonize new areas within a wood. Indeed it seems to have flourished in woods with long coppice cycles (about 20 years) in which areas of scrub blackthorn were cut back periodically, destroying established colonies but providing regenerating blackthorn for recolonization by the black hairstreak from elsewhere in the wood.

During this century numbers of known colonies have decreased from 60 to 30. This decline will almost certainly continue until the black hairstreak is restricted to areas where conservation measures are taken to ensure the provision of young blackthorn by cutting back old bushes. To help to ensure continuity of the black hairstreak only a small part of a thicket should be cut at a time, a measure not only enabling the transfer of the species from old to young thickets, but also preventing blackthorn from becoming moribund. The existence and survival of the black hairstreak is however incompatible with modern forestry, unless blackthorn thicket is retained and managed appropriately.

1.3 The woodland fritillaries.

The disappearance of several species of the closely related fritillaries (small pearl-bordered, *Boloria selene;* pearl-bordered, *Boloria euphrosyne;* silver-washed, *Argynnis paphia,* and high-brown, *Argynnis adippe*) from woodlands in eastern and central England has been perhaps the most striking change in the woodland butterfly fauna in recent years.

The study of their loss is only in its initial stages, but already it seems to be associated with trends in woodland management. Their larvae feed on violets, *Viola* spp, and are particularly associated with newly cleared woodland, where violets and other woodland herbs flourish. Understandably therefore this group of butterflies has suffered severely from the decline in coppicing, but the timing of their loss, over a relatively short period in the late 1950s and 1960s, additionally suggests that other factors are involved. For instance, the sudden loss of rabbits in the 1950s and the subsequent rank growth of woodland herbs, in the absence of grazing, might be expected to affect low-growing violets adversely.

The importance of coppicing to fritillaries is associated with the regular recreation of open habitats within a single wood or group of woods. These conditions may have been created recently in Monks Wood when the rides were widened but the chances of natural recolonization by one or more species of fritillary may be small because their nearest known source is now some 100 km distant.

1.4 Wood white *Leptidea sinapis* L.

Caterpillars of this species feed on a range of climbing or scrambling leguminous plants of which *Lathyrus pratensis* L. is probably the most important. These plants thrive in the rides of young conifer plantations which account for a large proportion of the current known habitats in England. The abundance of young plantations

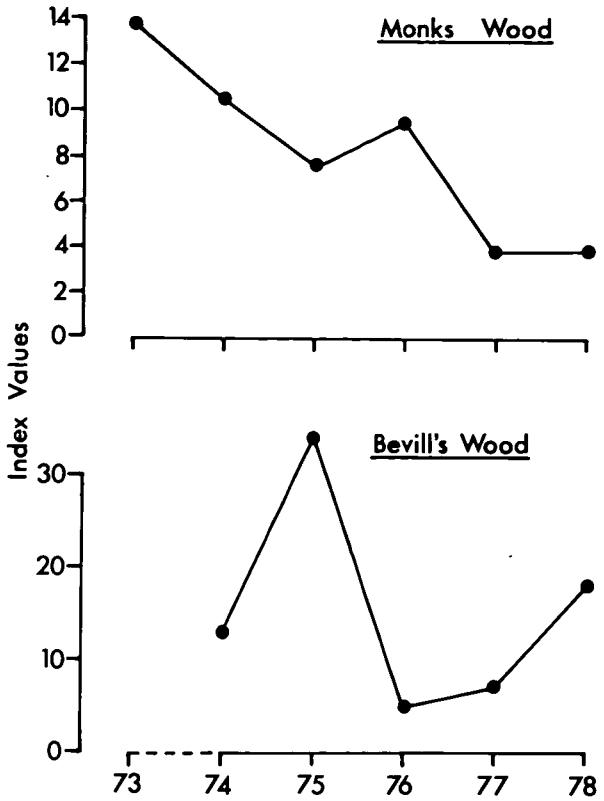

Fig. 52 *Index values (sums of the mean weekly counts) for the speckled wood* (Pararge aegeria) *at Monks Wood and Bevill's Wood.*

in lowland Britain may be the reason for the slight spread of this species in the last few years. At Monks Wood, outside its present breeding range and where suitable food-plants are scarce, 3 individuals have been recorded in the last 4 years. It is unlikely that the species will colonize Monks Wood, as food-plants are uncommon there, but it is possible that a nearby young Forestry Commission conifer plantation with abundant *Lathyrus pratensis* will be colonized.

2. Butterfly monitoring scheme

This discussion of woodland butterflies has usually been based on (i) knowledge of their general distribution (through the Biological Records Centre mapping scheme (Heath, 1973) and (ii) their biology and population ecology at specific sites. To understand the more general trends in numbers, a scheme coordinated at ITE Monks Wood for the Nature Conservancy Council has been initiated with the aim of monitoring butterfly abundance. It is based on weekly transect counts made along fixed routes (Pollard, 1977) at 60 sites including 19 woodland habitats. This national scheme was started in 1976 but records have been taken at (i) Monks Wood since 1973 and (ii) Bevill's Wood, a 20 years old Forestry Commission conifer plantation to the south of Monks Wood,

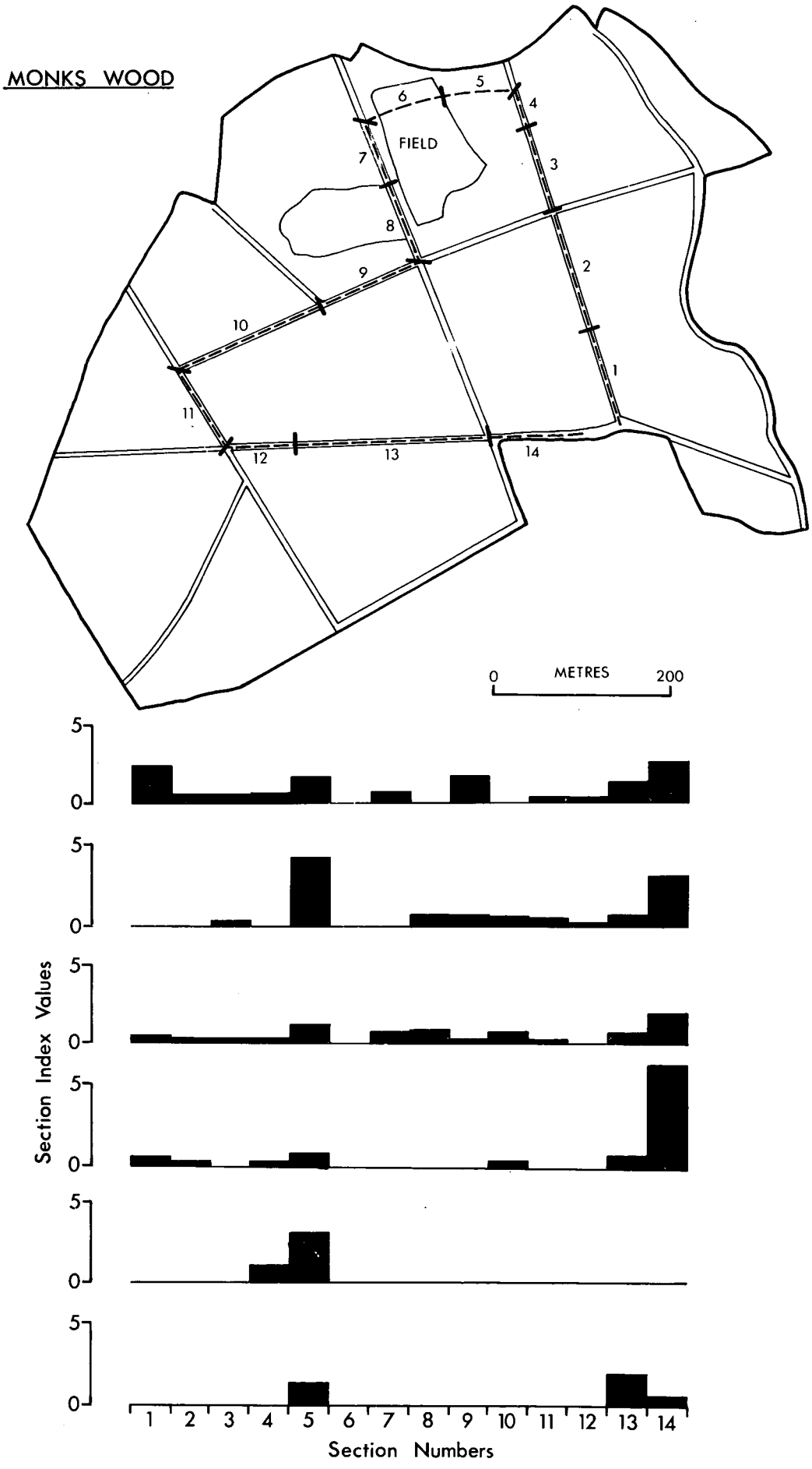

Fig. 53 *Section index values (sums of the mean weekly counts) for the speckled wood* (Parage aegeria) *at Monks Wood 1973-78.*

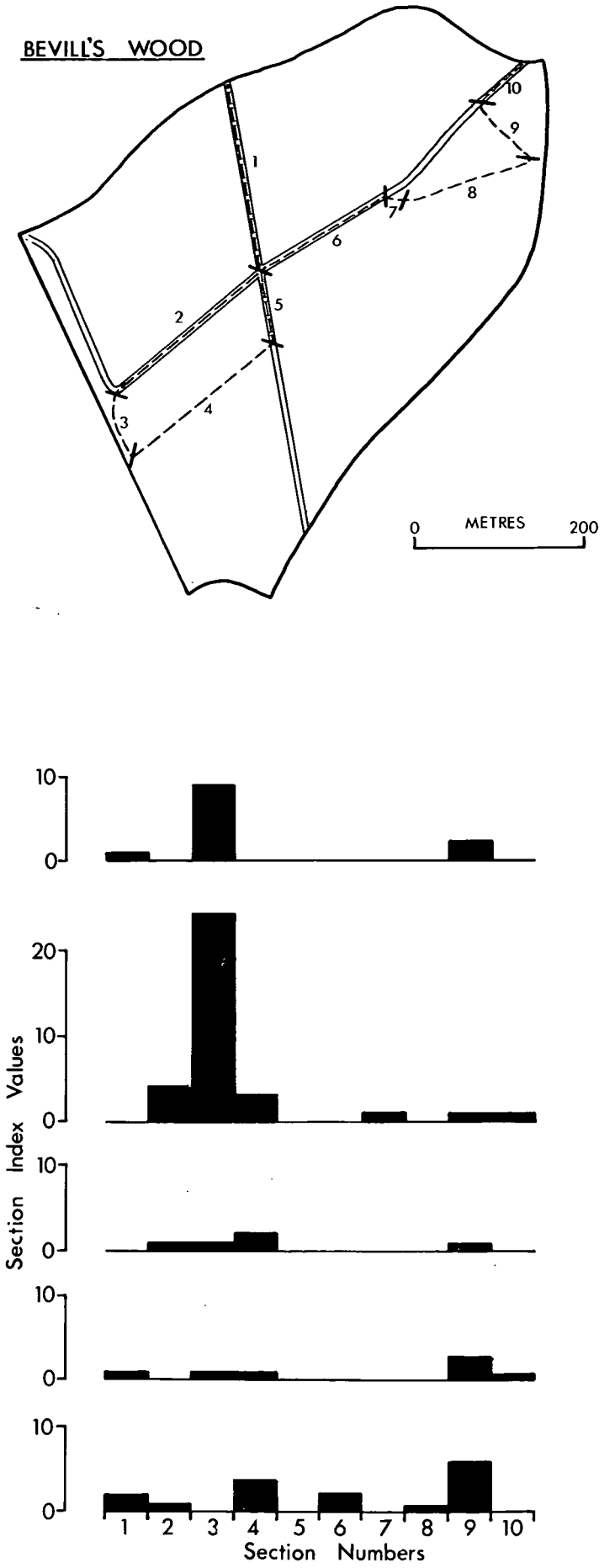

Fig.54 *Section index values (sums of the mean weekly counts) for the speckled wood* (Parage aegeria) *at Bevill's Wood 1974-78.*

since 1974. Although these periods of observation are short in relation to the timescale of woodland habitat changes, there is a discernible suggestion that the abundance of the shade loving speckled wood butterfly (*Parage aegeria* L.) has decreased at Monks Wood (Figure 52). On more detailed examination of transect data it seems that the speckled wood is becoming more widespread in the increasingly shaded Bevill's Wood whereas its distribution in Monks Wood is becoming less extensive as the number of shady rides has been reduced by management (Figures 53 and 54). In the former, the removal of deciduous scrub in 1975 was associated with a sharp decrease in the abundance of the speckled wood in 1976. The monitoring scheme may help us to identify changes in the fauna of a site while there is time to take action, before populations are seriously threatened.

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29. FACTORS AFFECTING THE BREEDING OF SPARROWHAWKS AND THE OCCURRENCE OF THEIR SONG-BIRD PREY IN WOODLANDS

I. NEWTON and D. MOSS

Associated with the agricultural use of organochlorine pesticides, numbers of sparrowhawks decreased drastically in most of Britain around 1960. Later, and as the use of these substances was increasingly restricted, populations of this non-migratory species of bird, which nests in woodland and feeds almost entirely on small birds, began to recover in some areas but not in others. To gain an understanding of the factors involved, detailed studies were made, mainly in southern Scotland, of their breeding behaviour and of some of the factors, notably afforestation, affecting the abundance of their song-bird prey.

1. Nesting densities and breeding success of sparrowhawks

Although they usually build new nests annually, sparrowhawks tend to nest in the same localities year after year, their nesting places being characterised by groups of nests of different ages usually within a radius of 50 m. In well-wooded districts, nesting areas were fairly regularly spaced, but distances between nesting areas differed greatly in different districts (Newton *et al.*, 1977). When comparing the distribution of nests in 12 parts of Britain, average distances between nesting areas (measured from the centres of the groups of nests) were found to range between 0.5 km on the low fertile land of the Solway Plain and 2.1 km on high barren land of the Upper Spey and Dee Valleys on the Cairngorm slopes (Table 43). These distances are equivalent to 24 nesting areas per 100 km^2 at the one extreme and 473 at the other. However, in reality overall densities were usually much lower because amounts of woodland suitable for nesting were limited. Numbers of nesting areas in the different districts varied between 14 and 96 per 100 km^2 when the mixtures of woodland and open land were taken into account (Table 43).

Average distances between nesting areas in continuous woodland were strongly correlated with (i) altitude above sea level, and (ii) soil productivity (Figure 55). Nesting areas were further apart on higher and poorer ground probably because there were fewer song-bird prey. When populations of song-birds were counted in different kinds of woods in 3 of the 12 districts studied, sparrowhawk nesting areas were found to be more widely spaced where song-birds were scarcest—a generalisation that is probably applicable throughout Britain. It suggests that numbers of breeding sparrowhawks are limited by amounts of suitable woodland, and numbers of prey (which influence spacing within woodland). The relationship with soil or altitude enabled predictions to be made of sparrowhawk spacing in woodland, merely by reference to maps. Not all nesting areas were used for breeding

TABLE 43 Spacing and densities of sparrowhawk nesting areas in different, but mainly upland, localities.

Locality	Numbers of nesting areas found at each locality	Mean distance to nearest neighbour in 'continuous' nesting habitat (km)	Theoretical* density in continous nesting habitat (pairs/100 km^2)	Actual density in whole district (pairs/100 km^2)
South Solway Plain, Cumberland	20	0.46	473	59
Annandale, Dumfriesshire	121	0.60	278	40
Eskdale, Dumfriesshire	50	0.62	260	79
Windsor, Berkshire	46	0.80	156	96
Lower Deeside, Aberdeenshire	16	0.91	121	89
Mid Deeside, Kincardineshire	36	1.12	78	49
Tregaron, Cardiganshire	22	1.28	61	31
Clashindarroch, Aberdeenshire	13	1.28	61	38
Upper Deeside, Aberdeenshire	9	1.39	52	45
Ae Forest, Dumfriesshire	29	1.55	42	43
Upper Speyside, Inverness-shire	42	2.03	24	14
Mar Forest, Aberdeenshire	9	2.06	24	21

* Assumes that entire 100 km^2 is composed of favourable habitat but this is rarely the case, woodland usually being interspersed with open spaces.

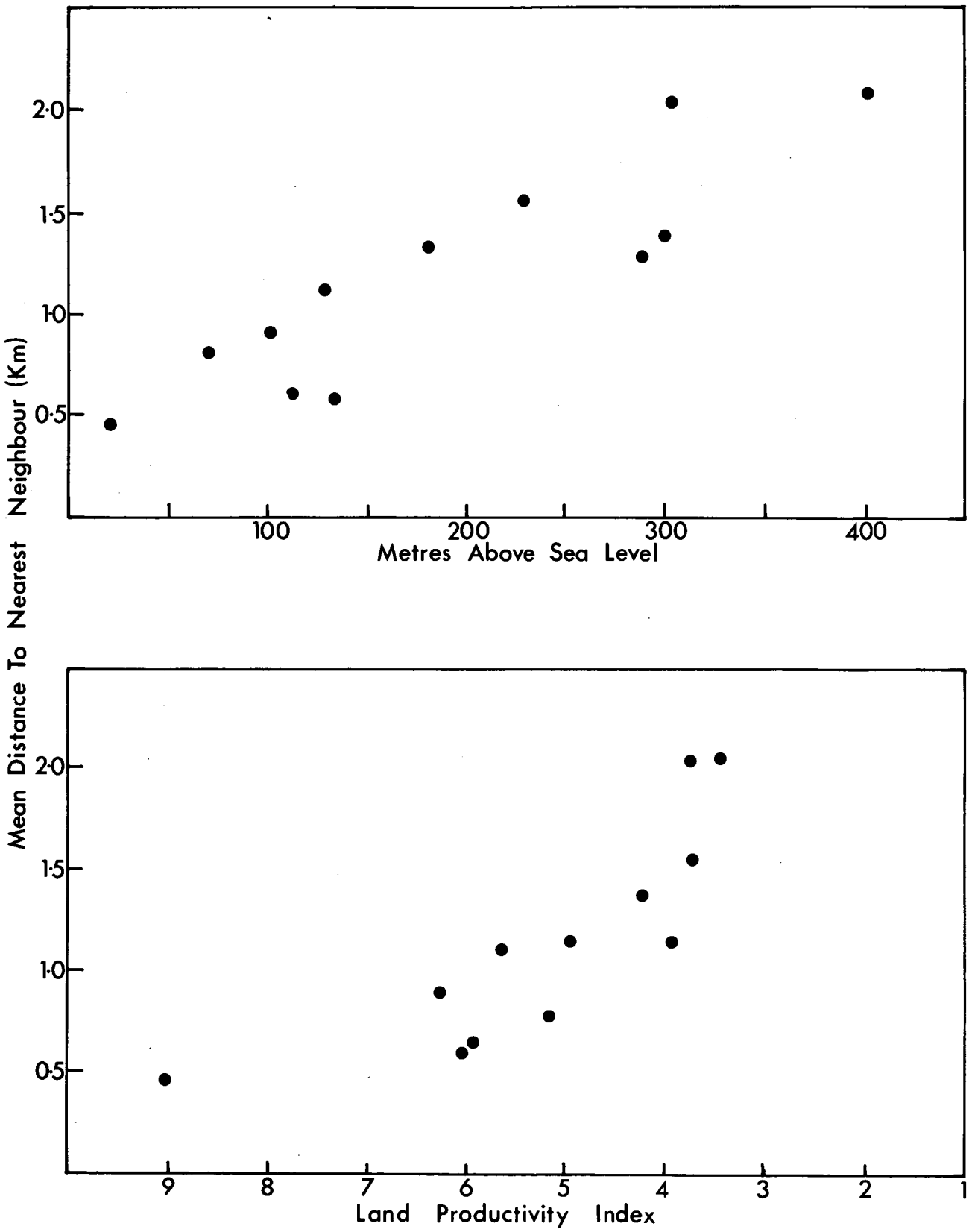

Fig. 55 *Mean nearest-neighbour distances of sparrowhawk nesting territories in continuous nesting habitat in relation to land productivity and altitude above sea level at 12 locations in the UK. The numbers 1 to 9 denote land of increasing productivity (Newton* et al., *1977).*

every year. In most districts the proportion ranged from 60 to 85% with extremes of 32% in one year in Upper Speyside and 91-97% in fair years near Windsor. These differences reflect the status of the different local populations which, in part, depends upon concentrations of organo-chlorine pesticides in prey species.

Before DDT was introduced, when sparrowhawks were more numerous, it seems that virtually all

nesting areas were used every year (Owen, 1916-22), the "space" occurring when a territorial bird was shot being quickly filled by another—this implied the presence of surplus birds in the population able to breed only when a nesting area was made available.

Breeding pairs defend their nesting areas, which could therefore be called nesting territories, but intermingle with other sparrowhawks in their hunting ranges, as was found by use of telemetric devices. They forage regularly in open habitats and in woodland. In rich habitats where prey was plentiful, sparrowhawks regularly hunted at distances of 3 km from their nests, but, in poor habitat, distances were increased to 9 km. Spacing and breeding success were thus influenced by conditions not only immediately around nesting areas, but also those in a much wider area, usually embracing several habitats.

The breeding success of sparrowhawks, like the spatial distribution of nesting areas, differed in different districts, depending partly on the local use of organo-chlorine insecticides and partly on prey abundance (Newton, 1976). The main 'organo-chlorines' found in sparrowhawk eggs were DDE (the principal metabolite of the insecticide DDT), PCB (from the industrial polychlorinated biphenyls) and HEOD (from the insecticides aldrin and dieldrin). The degree of shell-thinning, egg-breakage and addling were correlated with amounts of DDE in eggs; egg addling was also correlated with concentrations of PCB. No correlations were found with small concentrations of HEOD (Newton & Bogan, 1978). Other failures—some sparrowhawk pairs occupied nesting areas for a few days or weeks before leaving them whereas others laid eggs but deserted them—seem to be related to food shortages, being commoner in habitats where prey was scarce. Verification was obtained when the performance from nest-building onwards of sparrowhawks in poor habitats was improved, following the augmentation of their diet with carcasses of pigeons and other birds. These supplements increased the proportion of females laying eggs, numbers of eggs in each clutch and the survival of nestlings.

Summarising, breeding densities are limited by the extent of suitable woodland and the supply of food. However, in many districts populations are below these ceilings, partly because of the effects of organo-chlorines. Within woods, the distances between nesting areas are inversely proportional to the supply of prey. Breeding successes were similarly influenced by prey abundance and by amounts of 'organo-chlorines', which also differed between districts. Together, these factors account for many of the differences in breeding densities and success in different parts of Britain.

2. Populations of woodland song-birds

Partly because of their importance to sparrowhawks, numbers of song-birds were counted in a variety of habitats, including different types of woodland, using the so-called mapping method (Enemar, 1959; Williamson, 1964). Positions of song-birds encountered during each of 8 to 10 early morning visits per 'plot', spread over the period late March to mid-June, were marked on large scale maps and from the groups of positions numbers of territories of each species were estimated following the standardised rules of the International Bird Census Committee (1969).

2.1 Effects of coniferous plantations on populations in natural moorland and grassland

To estimate the effects of afforestation, bird populations on open sheepwalk and heather moor were compared with those in forests at different stages of growth. Nineteen sites (each 10-25 ha) were observed in the forests of Clatteringshaws, Ae and Eskdalemuir, all in south Scotland (Moss *et al.*, 1979), most being censused in at least 2 of the years in the period 1976-78 (Table 44). These results are summarised below:

Unplanted heather moor 2 breeding song-bird species (meadow pipit and skylark), with combined densities of 40-70 pairs/km^2.

'Natural' grassland, grazed by sheep The same common breeding species as on heather moor, but with increased combined densities of 70-130 pairs/km^2.

Plantation forest up to 8 years old These plots of young trees among rank grass or heather had more diverse structures than those of natural moor and grassland. Whereas skylarks were much scarcer, meadow pipits were more numerous, their numbers being augmented by new colonists to give combined densities of 125-200 pairs/km^2.

Pre-thicket plantations 12-14 years old Trees were touching, but closed canopies had not formed. Song-birds were more diverse (8-9 breeding species per plot) and more numerous than in younger plots, with combined densities of 230-290 pairs/km^2. Most incomers were scrub-dwelling species, with willow warbler and wren being the most abundant.

Thicket plantations, 23-27 years old Before thinning but after closed canopies had formed. Woodland species of song-birds, rather than scrub species, predominated, with 6-10 breeding species on each plot, and combined densities of 300-400 pairs/km^2. The goldcrest was the most abundant, followed by the chaffinch, wren, robin and coal tit.

TABLE 44 Densities (pairs/km^2) of song-birds on upland heather moor, grassland and Sitka spruce *(Picea sitchensis)* forests at different stages of growth (Moss *et al.*, 1979).

	Stages of afforestation					
	Unplanted heather moor	Unplanted grassland	Establishment	Pre-thicket	Thicket	Post-thinning plantation
Numbers of sites	2	3	5	2	3	4
Numbers of censuses	3	7	8	3	7	8
Song-bird densities (mean; range)						
Skylark	18*(13-20)*	51*(24-94)*	2*(0-4)*			
Meadow pipit	34*(25-53)*	37*(28-44)*	80*(44-122)*	15*(4-32)*		
Stonechat		1*(0-4)*	3*(0-10)*			
Wheatear		4*(0-12)*				
Wren			6*(0-29)*	69*(41-103)*	49*(28-83)*	89*(22-137)*
Chaffinch			3*(0-24)*	12*(9-17)*	88*(47-170)*	67*(33-91)*
Willow warbler			4*(0-23)*	67*(53-79)*	13*(0-42)*	1*(0-5)*
Redpoll			5*(0-23)*	18*(9-37)*		
Whitethroat			0*(0-3)*	1*(0-4)*		
Whinchat			5*(0-10)*			
Reed bunting			6*(0-17)*			
Grasshopper warbler			2*(0-7)*			
Goldcrest				31*(21-37)*	96*(59-156)*	113*(59-180)*
Robin				30*(21-43)*	42*(21-68)*	37*(14-67)*
Coal tit				8*(0-17)*	37*(28-48)*	47*(28-86)*
Dunnock				3*(0-9)*	6*(0-16)*	2*(0-9)*
Song thrush				3*(0-9)*	4*(0-10)*	3*(0-10)*
Mistle thrush					1*(0-5)*	1*(0-4)*
Chiffchaff					3*(0-3)*	5*(0-28)*
Bullfinch					2*(0-9)*	1*(0-5)*
Long-tailed tit					1*(0-9)*	1*(0-9)*
Crossbill					1*(0-10)*	1*(0-5)*
Siskin					3*(0-10)*	6*(0-22)*
Tree pipit					1*(0-10)*	
Tree-creeper						4*(0-11)*
TOTALS	51 *(38-72)*	93 *(72-130)*	115 *(54-203)*	257 *(231-289)*	347 *(302-443)*	377 *(318-425)*

Thinned plantations, 36-39 years old 6-10 species of breeding song-birds, with goldcrest, chaffinch, wren, robin and coal tit predominating: combined densities of 300-400 pairs/km^2.

As open ground gave way to forest, numbers and variety of breeding song-birds increased. Particular species came, and went, at different stages of forest growth (Figure 56). For example, the skylark began to decline immediately after planting, and had disappeared completely before the pre-thicket stage; the whinchat appeared late in the establishment stage and had gone before the thicket stage while the goldcrest appeared at the pre-thicket stage and became steadily more numerous as the forest grew. No one song-bird was present at all stages from open land to mature forest. Annual total numbers of species holding territories at some stage of forest growth were 24, 26 and 20 in 1976, 1977 and 1978 respectively.

Birds, other than song-birds, were more difficult to study. Several species disappeared at an early stage of forest development: ravens about the time of planting: curlews, other wader species and cuckoos before the pre-thicket stage: and merlins by the thicket stages (Marquiss *et al.*, 1978; Newton *et al.*, 1978). Other species including black grouse, short-eared owl, long-eared owl and barn owl, occurring on open ground or in mature forest, were especially numerous at the establishment and pre-thicket stages. The owls were attracted by the abundance of voles, but the long-eared and barn owls were limited by the availability of above-ground nest-sites, such as large trees, disused buildings or cliffs. From the thicket stage onwards, plantations were additionally colonised by jay, wood pigeon, woodcock, tawny owl and sparrow-hawk, adding to the numbers of crow and kestrel, which depended on openings, and water birds such as dipper and goosander which were present at all stages from open land to mature forest.

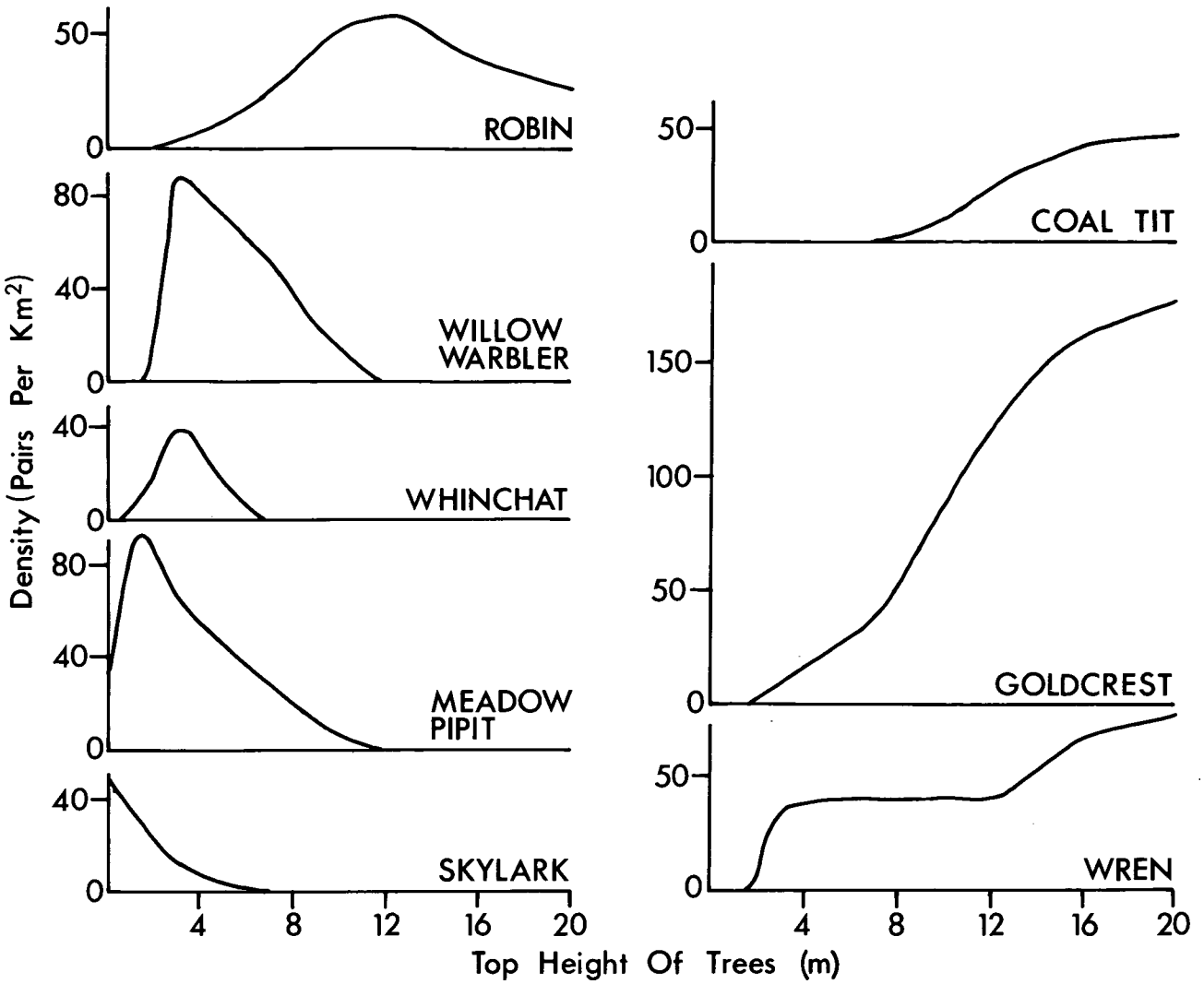

Fig.56 *The succession of song-bird species in ageing plantations of Sitka or Norway spruce, age being directly related to height.*

2.2 Bird populations in different types of mature woods (planted and semi-natural)

Censuses were usually made in 2 or more years of 15 sites (ranging from 4 to 14 ha) in Dumfriesshire and Inverness-shire, with natural or planted pine, larch, spruce or mixed deciduous trees (Table 45).

Even-aged pine stands, aged 40 years With variable ground layers but without a shrub-layer. 6-10 species of breeding song-birds with combined densities of *c* 200 pairs/km^2.

Semi-natural uneven-aged pine The one wood examined had a dense ground layer of heather and an understorey of juniper and birch. Same number of species as in even-aged planted stands of pine, but with *c* 400 pairs/km^2.

Self-regenerating pinewood, with some birch Trees and bushes of varying height and at irregular spacings; some small open areas. Relatively diverse array of song-birds, with up to 18 breeding species; combined densities in range 500 to 900 pairs/km^2 respectively.

Mixed deciduous wood, with few conifers A stand including a well developed understorey of shrubs and young trees, and some dead trees. 18 breeding species of song-birds and a combined density of *c* 1700 pairs/km^2.

Even-aged larch with small areas of spruce and Scots pine Song-bird population comparable to that in even-aged plots of spruce, but with fewer goldcrests counterbalanced by more wrens.

Even-aged spruce plantations, 25-50 years old Numbers of song-bird species, 4-9, similar in plots of Sitka and Norway spruces. Densities were larger in 1973-75 than in 1976-78 because of the greater densities of goldcrests in the earlier years.

The relation between woodland structure and the diversity of bird species in Dumfriesshire woodlands was quantified using (i) BSD, bird species diversity, a measure, calculated by the Shannon formula, of species numbers and the evenness of their distribution and (ii) FHD, foliage height diversity, an assessment of the distribution

TABLE 45 Densities (pairs/km^2) of song-birds in different types of mature woodland (Moss 1978*a*)

	Pine plantation	Semi-natural pine	Regenerating pine/birch	Mixed deciduous	Larch plantation	Spruce plantation
Number of plots	4	1	2	1	1	6
Number of censuses	6	2	4	2	2	11
Song-bird densities (mean; range)						
Blackbird			16*(13-17)*	59*(47-70)*		1*(0-6)*
Blackcap			2*(0-8)*			
Blue tit			19*(11-25)*	151*(116-186)*		
Bullfinch	1*(0-4)*	6*(0-11)*				0*(0-5)*
Chaffinch	55*(26-88)*	81*(66-95)*	103*(45-167)*	279*(256-302)*	78*(73-82)*	90*(59-145)*
Coal tit	39*(26-57)*	49*(46-52)*	29*(8-45)*	82*(70-93)*	56*(47-65)*	39*(20-59)*
Crested tit	4*(0-4)*	14*(11-17)*				
Crossbill		6*(0-11)*	3*(0-11)*			5*(0-11)*
Dunnock	1*(0-4)*	3*(0-6)*	2*(0-5)*			1*(0-9)*
Garden warbler			7*(5-8)*			
Goldcrest	41*(22-60)*	70*(57-83)*	38*(21-58)*	59*(47-70)*	113*(99-125)*	262*(136-417)*
Great spotted woodpecker			1*(0-5)*	6*(0-12)*		
Great tit			1*(0-4)*	82*(70-93)*		
Greenfinch				12*(0-23)*		
Jay			3*(0-5)*		5*(0-9)*	
Long-tailed tit			10*(4-13)*	23*(23-23)*	9*(0-17)*	
Mistle thrush	1*(0-4)*		1*(0-4)*	23*(23-23)*	5*(0-9)*	1*(0-9)*
Redpoll			6*(0-17)*			
Redstart				23*(23-23)*		
Reed bunting			4*(0-8)*			
Robin	15*(4-29)*	46*(43-49)*	89*(63-122)*	175*(140-209)*	39*(30-47)*	25*(5-53)*
Siskin	5*(0-17)*	26*(6-46)*				7*(0-29)*
Song thrush	1*(0-4)*	3*(0-6)*	12*(5-17)*	35*(23-47)*	5*(0-9)*	0*(0-5)*
Spotted flycatcher			1*(0-4)*	23*(23-23)*		
Starling				70*(70-70)*		
Tree-creeper	7*(0-16)*	14*(11-17)*	7*(0-16)*	70*(47-93)*	13*(9-17)*	7*(0-19)*
Tree pipit			1*(0-5)*			
Willow tit			16*(0-29)*	12*(0-23)*		
Willow warbler	4*(0-23)*	51*(46-55)*	196*(105-292)*	244*(209-279)*	9*(0-17)*	
Wren	38*(4-92)*	60*(57-63)*	116*(71-173)*	244*(186-302)*	119*(116-121)*	60*(0-100)*
Yellowhammer			1*(0-5)*			
TOTAL	207 *(151-340)*	428 *(385-471)*	685 *(463-935)*	1669 *(1593-1744)*	446 *(444-448)*	498 *(351-598)*

(spread) of foliage (= bird habitat) at different heights above ground. It was found that bird species diversity was directly proportional to FHD (Figure 57), probably because an increase in canopy complexity provides a greater variety of habitat (Moss, 1978*b*).

In general, the numbers of species and individuals were greater in stands with broadleaved trees than with conifers; among conifers, numbers of song-bird species were greater in spruce than pine. Mixed woods, containing mainly broadleaved trees but with some conifers, were richer than stands with either broadleaved or coniferous species. Other factors being equal, densities of birds were generally much greater in stands of trees growing on increasingly productive soils, the effect being attributable to numbers of individuals which increased and not to numbers of species. Von Haartman (1971) recorded increases of x3-6 in parts of northern Europe with increase in soil productivity. Possibly because of the so-called "edge effect", densities of song-birds in small woods in open land were usually greater than in equivalent areas in larger forests. However, species diversity was often less in small woods than in large ones (Moore & Hooper, 1975).

Compared with other mature woodlands, even-aged stands of conifers have fewer species of song-birds, and fewer individuals of each species, than do broadleaved or mixed woods, or woods of any kind with a shrub layer. However, they have more diverse arrays than are found on moorland and natural sheepwalk. Notwithstanding these conclusions, more observations need to be taken in

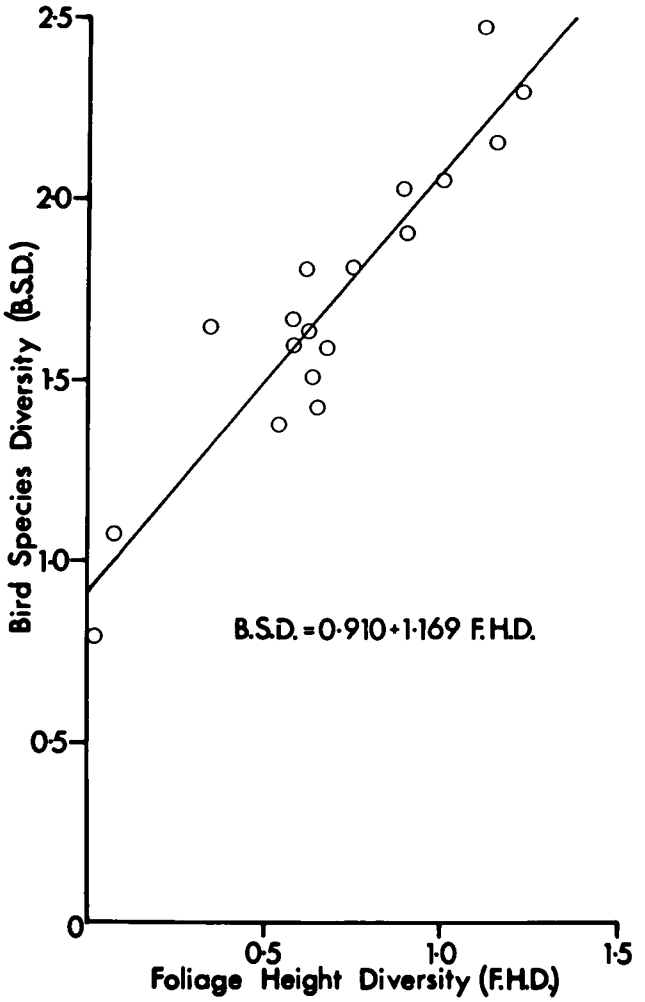

Fig. 57 *Relationship between bird species diversity and foliage height diversity when examining a variety of mature woods with broadleaved or coniferous species or mixtures.*

other parts of Britain including (i) greater numbers of semi-natural woods, (ii) the effects of windthrow and clear-felling and (iii) censuses of waders and other large birds not properly covered in the work already done.

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30. GREY SQUIRREL DAMAGE AND MANAGEMENT

R.E. KENWARD

Grey squirrels *(Sciurus carolinensis)* became established in Britain after being released at several sites between 1876 and 1910 (Middleton, 1931). They now occur in lowland woodlands in most of the country, largely replacing the native red squirrel *(Sciurus vulgaris).* Since the 1930s, grey squirrels have been considered as pests, partly because of damage they do to stored grain, fruits, vegetables and wild life, but mainly because of sporadic episodes when forest and woodland trees are subject to severe bark-stripping (Shorten, 1957, 1962). The growth of the worst affected trees, typically sycamore *(Acer pseudoplatanus),* beech *(Fagus sylvatica)* and oak (*Quercus* spp.), may be stunted as a result of stem ring-barking with subsequent death of the upper crown; when bark removal is extensive trees may be killed outright. Removal of lesser quantities of bark may decrease timber quality and possibly facilitate colonisation by fungi (Plates 22 and 23).

1. Past and present

At first it was thought that the damaging grey squirrel could be exterminated from Britain, but a bounty scheme to encourage its eradication prevented neither the spread of squirrels nor their damage. Since bounty payments were abandoned in 1958 (Thompson & Peace, 1962), attempts at control have been organised locally (Rowe, 1973), trapping proving to be more effective than shooting (Taylor, 1963). In 1973, a Parliamentary Order permitted the use of hoppers containing warfarin-treated grain. However, bark-stripping is not always prevented by reduction of a local squirrel population, and a drawing-in of squirrels to bait may even temporarily increase damage (Taylor, 1966, 1969). Moreover, other species are susceptible to poisoning, either directly from hoppers (Wood & Phillipson, 1977), or perhaps secondarily by eating dead squirrels (Marstrand, 1974).

An understanding of why a species causes damage can sometimes help the development of effective prevention techniques. At least 9 suggestions have been advanced to explain why grey squirrels strip bark: shortages of food or water, trace nutrient deficiencies, a liking for sweet sap, the collection of nest material, a persistent gnawing reflex, the prevention of incisor overgrowth, and agonistic display or territorial boundary marking (Allen, 1943; Shorten, 1954; Taylor 1966; Davidson & Adams, 1973). Of these suggestions 4 can be discarded:

a) Water shortage is an unlikely cause of bark-stripping, because trees by open water are stripped (Seymour, 1961); furthermore, damage to woodlands during the wet summers of 1977 and 1978 was sometimes severe.

b) Squirrel dreys are lined with bark finer than that from tree stems, which is dropped to the ground (Shorten, 1954).

c) Instead of a territorial social structure, squirrels have a dominance hierarchy (Taylor, 1969; Thompson, 1978) with bark-stripping not always occurring where boundaries might be expected.

d) Tooth wear is minimal because bark is removed by pulling instead of gnawing. Thus, bark-stripping is unlikely either to decrease incisor overgrowth or to result from a simple gnawing reflex. After bark stripping, squirrels scrape and eat the soft sap-containing vascular tissues (Taylor, 1969).

In contrast, there is evidence to support the 'agonistic display' and food shortage theories. Bark damage in Britain is seasonally most severe during mid-summer, when small body weights, diverse diets and the ready acceptability of bait suggest food shortages, bark damage often occurring in supposedly poor habitats (Taylor, 1969); squirrels observed bark-stripping by Taylor were nearly all juveniles or subadults (1 year old). Mid-summer is also a time when squirrels disperse and when agonistic encounters, which may include gnawing, occur most commonly. Taylor has suggested that bark-stripping is caused by inferior squirrels which move into inadequate habitat and engage in agonistic gnawing while establishing a social order, so discovering that sap is an acceptable food. But, because the sap appears to have a small energy content (D.A. Wood, pers. comm.) food shortage is unlikely to be the only factor causing extensive bark-stripping. In an oak-maple plantation in Minnesota, bark-stripping occurred even when acorns were available (Irving & Beer, 1963); in another instance, the provision of food did not prevent similar damage by fox squirrels *(Sciurus niger)* (Allen, 1943); in Britain, cambium was found in the stomachs of adults and individuals with large body weights shot in a damaged area (MacKinnon, 1976). However, sap, because of its sugar content, might be preferred food. Amounts of assimilable sugars are maximal in sycamore sap in mid-summer (Cockerham, 1930), this species, *A. pseudoplatanus,* being congeneric with the sugar maples *(Acer saccharum)* which appear to be "limited by incessant squirrel damage" in some parts of the USA (Brenneman, 1954). Nevertheless, a preference for a low-energy food would seem inappropriate. If this is so, sap containing tissues may be eaten to obtain one or more temporarily deficient trace nutrients.

If and when the causes of bark-stripping are known, it may be possible to improve squirrel management with the evolution of new methods of control. If immigration causes agonistic encounters which trigger extensive bark-stripping, then the recommended practice of decreasing squirrel numbers in damage-prone areas during spring may not only be ineffectual, but also counter-productive, because reducing the resident squirrel population could increase immigration (Taylor, 1969). A more effective method might be to reduce squirrel populations in good habitats adjacent to vulnerable areas. If food shortages were responsible for extensive bark-stripping, the level of damage might be predicted by relating spring squirrel populations with food availability. If the need for a trace nutrient were the cause of damage, perhaps the deficiency could be minimized artificially, eg by providing a 'squirrel-lick' which could become the basis of a new and possibly selective method of trapping and which would not jeopardize other wildlife.

2. The future

Five approaches are envisaged including removal experiments, radio-tagging, analysis of (i) stomach contents and (ii) plant vascular tissue composition, and experiments with captive squirrels.

2.1 Removal experiments These will be done in 2 woodland areas each with mature oak and ash and adjacent to young plantations in which beech, oak and sycamore were damaged by squirrels in 1977 and 1978. In one set of locations, the controls, the natural course of events will be followed. In the other, some, but not all, of the squirrels will be removed from the young plantation so as to investigate effects of the remnant population on immigrating squirrels, their nutritional condition and bark-stripping activities. If removal of squirrels from a damage-prone young plantation, with adjacent mature woodland, increases immigration or otherwise favours bark-stripping, then effects of removing squirrels from the mature woodland will be investigated.

2.2 Radio-tagging In the control area of the removal experiment, some squirrels will be fitted with collars having radio transmitters so that their movements can be readily monitored without the need for baited traps, which may themselves influence feeding patterns. Radiotagging will also be used to identify the age, sex, body weight, range size and activity of individual squirrels so facilitating comparisons between those that do, and do not, strip bark. A radio receiver, which can be programmed to scan each transmitter frequency in turn for several seconds and which records automatically on paper tape, will be mounted at the base of trees subject to stripping so that the squirrels responsible can be identified and their periods of activity recorded. At present, the radio-collars are being tested to see if they adversely affect squirrels and their movements, comparisons being made with others marked by toe-clipping. By 22 October 1978 6 transmitters had been 'worn' for a total of 298 days without a death. Transmitter ranges in woodland are about 400 m and 1 km when squirrels are on the ground or in trees respectively.

2.3 Analyses of stomach contents The stomach contents and condition of dead squirrels from damaged woodlands will be analysed to see if dietary deficiencies can be detected.

2.4 Sap composition The content of sugar and of other nutrients in vascular tissue samples from damaged and undamaged trees will be analysed.

2.5 Experiments with captive squirrels Hand-reared squirrels will be kept in an enclosure for attempts to develop traps which selectively capture bark-stripping squirrels. If wild squirrels that strip bark appear to be short of major or minor nutrients, the diets of captive squirrels could be manipulated in an attempt to induce bark-stripping, with the possibility of diet supplementation trials in the wild.

While the work just outlined is being done, B. Don at Oxford University will be adopting a different approach to the squirrel problem. He will be studying relationships between woodland structure and squirrel damage to see if forest management can play a part. The role of NERC in conservation research is well known, usually in the context of protecting species and habitats. In the event the conservation of species such as beech, oak and sycamore may necessitate the local destruction of another species, namely the grey squirrel.

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31. ABUNDANCE OF FIELD VOLES *(MICROTUS AGRESTIS)* IN CONIFER PLANTATIONS

W.N. CHARLES

Field voles *(Microtus agrestis)*, which live in grassland, are the most abundant rodent in the uplands of Britain where they are an important prey species for foxes *(Vulpes vulpes)*, stoats *(Mustela erminea)*, weasels *(Mustela nivalis)*, short-eared owls *(Asio flammeus)*, long-eared owls *(Asio otus)* and kestrels *(Falco tinnunculus)*.

When open ground is fenced, drained and planted with conifers, the standing crop of ground vegetation temporarily increases with concomitant increases in voles. However, after a period of 10-15 years numbers of voles decrease as the growth of the ground layer is deleteriously affected by shading. During this time, vole populations fluctuate from year to year and cyclically reach peaks every 4-6 years (Chitty, 1952) often exceeding 1000 ha^{-1} compared with minima of *c* 5 ha^{-1}. Occasional exceptionally dense populations have been recorded (*c* 2-3000 ha^{-1}) as at the Carron Valley in central Scotland in 1952-53 when the bark of young trees was stripped (Charles, 1956). However, extensive damage is infrequent, the field vole not usually being regarded as an important economic pest of British forests.

1. Assessment

Although the dynamics of many separate populations have been measured in geographically restricted areas of young forests, less is known about their fluctuations on a more extensive scale. Because populations of predators seem, understandably, to reflect those of their vole prey (Lockie, 1955), studies were initiated to record (i) how field voles respond to different types and grades of habitat within, and adjacent to, young forests and (ii) whether changes in different areas are synchronous. Populations of voles have been assessed from 1975 to 1978 inclusively, in 3 habitats (i) open hill, (ii) young conifer plantations, 3-10 years after planting, and (iii) closed conifer plantations, > 20 years after planting, in each of 2 regions of Scotland with considerable amounts of recent afforestation– Eskdale in the Borders, and Galloway in the south-west. In the former, a 'rich' area, the schists are mostly covered by grass whereas at the latter, a 'poor' area, the granitic bedrock has a cover of heaths and bogs. In each region, samples were taken from 3 replicate areas of each type of habitat, blocks of open unplanted ground and young forest usually measuring 10 ha, and 5-15 ha

TABLE 46 Estimated effects of afforestation on populations of voles in 2 areas of Scotland. (Numbers of voles ha^{-1}, 1975/78).

Type of habitat	Areas of Scotland	
	Eskdale	Galloway
Unplanted open hill	<5	10
Young forest, planted 1968-73	130	50
Closed forest, planted before 1960		
(i) Rides	15	18
(ii) Planted areas	<5	<5

respectively. At Eskdale it was also possible to assess in greater detail the effects of differing planting dates in the period 1969-72.

Estimates of vole abundance were obtained in the spring and autumn of each season by using randomly arranged series of snap traps in each study area. Simultaneously, the relative abundance of different ground cover plants was estimated, together with the heights of trees of different species.

2. Progress

Although the data have not been fully analysed, it seems that:–

a) densities of voles in open ground, which rarely exceeded 10 ha^{-1}, were similar in both Eskdale and Galloway (Table 46),

b) during the early stages of afforestation (years 1 to 5), numbers of voles increased to about 130 ha^{-1} and 50 ha^{-1} at Eskdale and Galloway respectively,

c) numbers of voles averaged 5 ha^{-1}, in closed forests, and they were probably absent in some areas,

d) more voles occurred in the rides (15-18 ha^{-1}), than in the planted areas of closed forests,

e) populations of voles varied seasonally being largest in autumn, at the end of the breeding season, and least in spring before breeding commenced (Figure 58). Densities were largest in 1975 and least in spring 1977.

f) mean numbers in different compartments ranged from 23 to 280 ha^{-1}, the former on blanket peat with *Calluna vulgaris* dominant and the latter on mineral soils with *Agrostis* spp dominant,

g) the population shifts in most of the 16 forest compartments measured at Eskdale, some being 15 km apart, were synchronous.

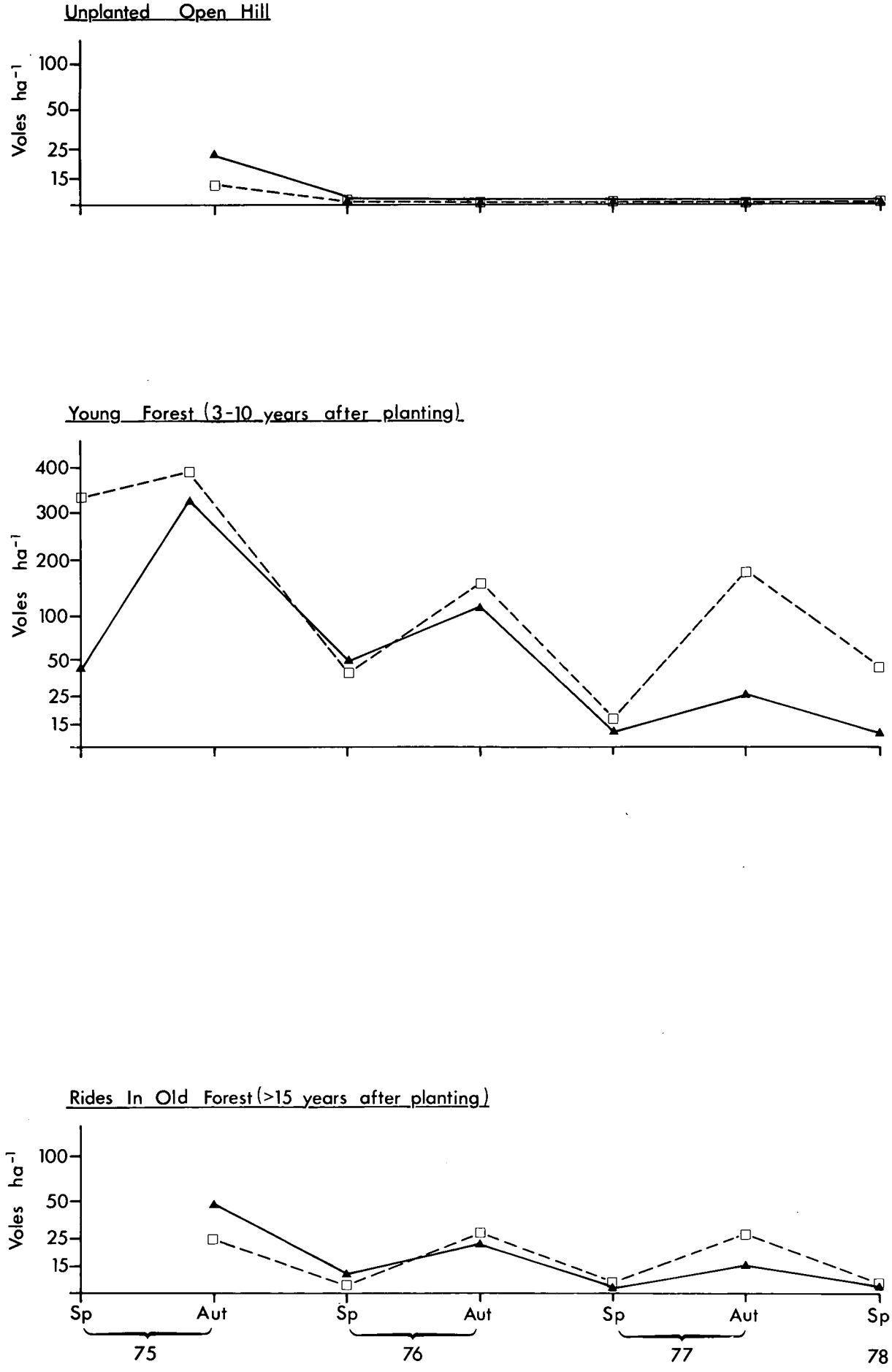

Fig. 58 *Changing populations of voles* (Microtus agrestis), *plotted on logarithmic scales, in open hill, young and old forests in Eskdale (— — —) and Galloway (———), Scotland.*

Already it has been possible to identify seasonal influences on the populations of voles which increase immediately after afforesting open hill and later decrease as conifers impose shade on the layer of ground vegetation. Interestingly, the annual changes seem to be synchronous over extensive areas but more observations are required to characterise the geographical extent of this response. These studies were supported by an intensive examination of the changes in avian predators in Eskdale by A. Village, formerly of Edinburgh University, who was mainly concerned with kestrels.

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32. DEER AND THEIR WOODLAND HABITATS

B.W. STAINES and D. WELCH

In Britain, 6 species of deer are found in woodland habitats (Table 47). Whereas the Chinese water deer *(Hydropotes inermis)* is restricted to south-east England, the others are more widespread, with red deer *(Cervus elaphus)* and roe deer *(Capreolus capreolus)* being abundant and nationally important.

Although red and roe deer have intrinsic value as wildlife and are sporting assets, they are also regarded as pest species, the former more particularly in the highlands of Scotland. Both species alter the composition, or prevent the regeneration, of many semi-natural woodlands, and additionally damage plantation trees by browsing and bark-stripping. Red deer, probably because of their larger size and tendency to herd, are generally regarded as the greater threat. The demand for shooting is increasing, particularly from sportsmen in continental Europe; the cost to shoot red deer stags in 1978 ranged from £75 - £300 and of roe bucks from £40 - £250. The price paid for venison in 1979/80 varied, but was usually from £1.43 - £1.76 kg^{-1} for red deer and £1.65 - £1.87 kg^{-1} for roe.

1. Red deer

Red deer are most numerous on open-hill ground in Scotland. In winter, they seek lower ground for food and shelter, and it is then that they may break into plantations or occupy semi-natural woods of conservation interest, frequently causing damage. Increasingly, however, they are becoming permanently resident in plantations, and, as a result, are posing new management problems. Red deer are social and gregarious animals. Hinds and stags segregate for most of the year, often into separate areas. Individuals have overlapping home ranges (Lowe, 1966) and generally join with others to form groups. These aspects of social organisation differ according to habitat, with group sizes and home ranges being smallest in woodlands and largest in open country (Staines, 1974). Animal

TABLE 47 Deer species found in British woodlands and problems of management.

Species	Distribution	Management problems and conservation interest
Chinese water deer *(Hydropotes inermis)*	Local in East Anglia, Bedfordshire and Hertfordshire	Small and probably decreasing numbers give cause for concern for its future.
Muntjac (*Muntiacus* spp)	Increasing numbers and range in southern and central England.	No important management problems obvious.
Fallow *(Dama dama)*	Widespread throughout southern and central England. Local populations in Wales, northern England and Scotland.	Browsing in plantations. Damage to farm crops and possible competition with livestock. Some local populations of special interest (eg Epping Forest, Mortimer Forest).
Sika *(Cervus nippon)*	Local populations scattered throughout Great Britain, locally abundant and thought to be increasing.	Browsing and bark-stripping in plantations. Hybridises in some areas with red deer.
Roe* *(Capreolus capreolus)*	Widespread and abundant in Britain apart from central England.	Browsing in plantations. Fraying of saplings by bucks and some bark-stripping. Affects regeneration of semi-natural woodland.
Red* *(Cervus elaphus)*	Widespread and abundant in the highlands and islands of Scotland. Locally large populations elsewhere, eg in north-west England and south-west Scotland.	Browsing and bark-stripping in plantations. Affects regeneration of semi-natural woodlands and other plant communities and species. Damage to farm crops. Local small populations of special interest (e.g. New Forest). Hybridisation with Sika influencing genetic make-up locally (eg NW England).

* 2 indigenous species

performance is similarly variable. On hill ground, hinds frequently grow slowly and rarely become sexually mature until 2 years 4 months; the annual recruitment of calves is only about 1/3 of the total adult stock. Current work by the Forestry Commission suggests that performance in plantations can be much better, with puberty one year earlier and fertility and growth rates much higher. Clearly culling levels based on data from the relatively poor hill populations will be inappropriate for controlling the more fecund woodland deer.

2. Roe deer

These animals are generally year-round occupiers of woodland, and have been studied most in this habitat; unlike red deer, they are rarely gregarious. From April to August, some bucks are territorial, territory size ranging from 8 ha - 128 ha according to locality and habitat (Bobek, 1977); non-territorial bucks have larger ranges which may overlap with those of other bucks, or they may be found in peripheral areas. If they are unable to establish a territory, they are not generally

TABLE 48 Ranked red deer preferences in different countries for different types of tree browse (Mitchell *et al.*, 1977). Where names are restricted to genus, the original authors either did not distinguish between species or did not give sufficient information to enable species to be determined.

Ranked preferences	White Russia	Poland	Poland*	West Germany	S Sweden	NW England
Highly preferred	*Salix* *Populus tremula* *Fraxinus* *Quercus*	*Quercus petraea* *Salix caprea* *Sorbus aucuparia* *Corylus avellana*	*Populus tremula* *Salix caprea* *Frangula alnus*	*Populus tremula* *Quercus borealis* *Abies* *Acer platanoides* *Fraxinus excelsior* *Quercus*	*Fraxinus excelsior* *Salix* *Frangula alnus*	*Juniperus communis* *Quercus borealis* *Pinus contorta* *Picea abies*
Preferred	*Sorbus aucuparia* *Betula*	*Acer platanoides* *Carpinus betulus* *Prunus serotina* *Frangula alnus*	*Quercus robur*	*Pinus sylvestris* *Picea abies* *Fagus sylvatica* *Pseudotsuga menziesii* *Larix*	*Betula*	*Larix* *Acer pseudo-platanus* *Pinus sylvestris* *Quercus robur* agg *Betula*
Seldom or never browsed	*Tilia* *Carpinus betulus*	*Pinus sylvestris* *Juniperus communis*	*Tilia cordata* *Carpinus betulus* *Betula*	*Picea sitchensis* *Alnus glutinosa* *Betula*	*Alnus glutinosa*	*Picea sitchensis* *Fagus sylvatica* *Alnus glutinosa*

* includes roe deer browsing.

Red deer are "intermediate" feeders (Hofmann, 1973), taking browse and grasses in varying amounts according to locality and season. There is sparse information on food preferences in British woodlands, but observations from better quality forests in continental Europe suggest that deciduous browse is the most preferred food, aspens and various species of willows being particularly favoured (Table 48). Browsing seems to be an important, natural feature of deer biology and is unlikely to be, as sometimes intimated, a pathological form of behaviour. To satisfy their requirements for growth, maintenance and reproduction, an "average" deer may consume 4 kg dry matter per day (Mitchell *et al.*, 1977).

seen again in the same area in subsequent years (Bramley, 1970). In the short term, at least, territories are traditional, and, when a territory is vacated (eg as a result of shooting), it may be quickly acquired by a new incoming buck, less frequently being absorbed into the territories of neighbouring animals (Bramley, 1972). Does have overlapping home ranges which may overlap the ranges of one or more territorial bucks. There is evidence to suggest that a yearling is prevented by social interaction from establishing its range within that of its mother (Bramley, 1972; Strandgaard, 1972), and, as a result, young animals emigrate. Because of this pattern of

behaviour, culling policies should be applied over a wide area, otherwise heavy shooting in one locality will be counteracted by immigration from neighbouring places where the cull is less than equal to the rate of recruitment. Recently, attempts have been made to relate territory and range size to habitat features or quality, so far with inconclusive results (eg Bobek, 1977; Hosey, 1974). But if, as is likely, habitat features are the determinants of overall density, then it is essential that these features should be better understood for the development of better management techniques.

Roe deer take more browse and forbs than red deer, although grasses are eaten to a limited extent in summer (Siuda *et al.,* 1969). The bucks may also damage saplings by fraying when they hold or take up territories (spring to mid-summer).

3. Effects of deer on forests and forest structure

What is 'damage'? Although all browsing and bark-stripping can be regarded as biological damage, concern is usually expressed only when timber production and/or quality is affected, or when regeneration is seriously jeopardised.

3.1 Semi-natural woodlands

In these habitats, the main problem relates to regeneration. In many woodlands, and particularly native Caledonian pine forests, regeneration is being prevented by the heavy browsing of seedlings and saplings by relatively large numbers of deer. Although these animals may not have been the main cause of the decline in areas of semi-natural woodland in upland Britain, there is little doubt that present-day populations, particularly of red deer in winter, thwart re-establishment even where conditions are otherwise favourable. In addition, deer affect woodland composition. Because they graze selectively, some species of trees are more vulnerable than others (Table 48), and may be eliminated from the ground flora or as sub-dominant trees; indeed, there are few species of tree, apart from the dominants, in many grazed woods in Scotland. The moral is obvious; if diversity is a priority, then there must be lower numbers of deer than if we merely wish to maintain the presence of woodland.

3.2 Plantation forests

The growth of young trees, up to about 2 m tall, can be adversely affected by the loss of leaders and side shoots from browsing, and larger trees are endangered by bark stripping, but how much apparent damage can be tolerated? What is acceptable to one person may be regarded as disastrous by another, and, because many years may elapse between the occurrence of damage and the harvesting of the final crop, it is not easy to assess the yield reductions and financial losses. It is necessary also to put the impact of deer into perspective with other factors that continuously or spasmodically reduce yields, such as invertebrate pests, nutrient deficiencies, climatic extremes and windblow. Sometimes, the latter mask the effects of deer; sometimes, they exacerbate them, eg slow-growing young trees are vulnerable to browsing for longer periods than more rapidly-growing specimens. Forest managers can do little to control some of the causes of damage, but, because numbers of deer can be altered and because income can be obtained when the stalking rights are leased, it is desirable to define the optimal densities at which to maintain populations of deer, a definition that must take account of many complexities. During the 3 or 4-year period following the removal of leaders by browsing, tree growth may be noticeably retarded, but should it be inferred that the final crop will be deleteriously affected? Damage to one tree may decrease the effects of competition on its neighbours which may therefore grow more rapidly. Furthermore, the herbivores may reduce the competitiveness of the ground vegetation, allowing the entire population of trees to grow more rapidly, as in orchards when herbicides are used to restrict growth of grass and herbs; browsing may also be analagous to pruning and cause better root development in crop trees. The effects of browsing need to be monitored over longer periods than hitherto, preferably with concomitant measurements of animal utilisation and density. In this way, it should be possible to get a better balanced assessment of the expense of deer control in relation to crop yield (Plate 24).

Bark stripping is possibly a more serious problem than browsing because trees are susceptible to stripping for longer periods (Mitchell *et al.,* 1977). At present, it is bark-stripping by red deer that causes concern, but we now know that roe and Sika deer also eat bark, and, potentially, their effects are equally serious. Severe stripping just once in 20 years, or the repeated occurrence of less intense stripping can both substantially damage tree crops, depending on how the trees respond to wounding. Growth may be retarded and timber defects caused, but openings are also provided for colonization by pathogens which degrade the structural properties of timber and increase the risks of "snapping" in windy and snowy conditions. Again, how does this damage compare with other forms of damage, such as that done when extracting timber?

Although Sitka spruce is less vulnerable to bark-stripping than many other conifers (Table 49), it could become more susceptible if populations of other, more vulnerable tree species are deliberately decreased as a result of positive manage-

TABLE 49 Ranked susceptibility of trees to bark-stripping by red deer in different countries (Mitchell *et al.*, 1977) Where names are restricted to genus, the original authors either did not distinguish between species or did not give sufficient information to enable species to be determined.

	White Russia	East Germany	West Germany	Denmark	Galloway, SW Scotland	NW England
Highly susceptible	*Salix* *Fraxinus*	*Picea abies* *Fraxinus excelsior* *Pseudotsuga menziesii*	*Picea abies* *Fraxinus excelsior* *Salix* *Populus*	*Picea abies* *Pinus contorta* *Pinus mugo* *Pinus sylvestris*	*Pinus contorta* *Pinus sylvestris*	*Pinus contorta* *Pinus sylvestris* *Picea abies*
Moderately susceptible	*Alnus incana* *Sorbus aucuparia* *Quercus* *Pinus sylvestris* *Picea abies* *Betula*	*Fagus sylvatica* *Abies* *Pinus sylvestris* *Acer*	*Pseudotsuga menziesii* *Tilia* *Pinus sylvestris* *Fagus sylvatica* *Larix* *Sorbus aucuparia* *Acer pseudoplatanus*	*Larix decidua* *Larix leptolepis* *Pseudotsuga menziesii* *Picea sitchensis* *Abies alba* *Abies grandis*	*Larix decidua* *Larix x eurolepis* *Larix kaempferi* *Picea abies*	*Pseudotsuga* *Larix leptolepis* *Larix decidua*
Seldom affected	*Tilia* *Carpinus betulus*	*Quercus*	*Abies* *Quercus robur* agg *Alnus glutinosa* *Betula*		*Picea sitchensis*	*Picea sitchensis*

ment decisions, or if the frequency and size of open feeding areas are progressively decreased. In the north of Scotland, the increasingly extensive planting of *Pinus contorta* may also be jeopardized, as this species is very vulnerable to stripping (Plate 25).

The structure and composition of woodlands undoubtedly influence the behaviour and performance of resident deer. Newly afforested areas, and areas in the early stages of re-afforestation, provide food but offer little cover for deer until trees are 1.5 m tall. Thereafter, the amount of cover increases rapidly, but, as the thicket stage is reached, amounts of available forage decrease. In Sitka spruce plantations, food continues to be scarce for the next 20 years, but, with the transition from the pole stage to high forest and with the removal of thinnings, the cover value decreases, whereas food availability increases, albeit slightly.

TABLE 50 Outline of the integrated programme of woodland research being done by ITE, the Forestry Commission (FC) and the Red Deer Commission (RDC).

	FC	RDC	ITE
1. Deer distribution and behaviour	–	+	+
2. Quantification of damage and its biological and economic effects	+	+	+
3. 'Census' technique	+	+	+
4. Longer term woodland management (including plantation design, silvicultural systems)	+	–	–
5. Management of red deer as a resource	+	–	–
6. Red deer population dynamics	+	–	+
7. Shorter term woodland management (including deer-related management techniques, control and plantation protection)	+	+	–

Within a forest, the mosaic of habitat types depends on successional planting dates, local site factors and silvicultural practice, and, to guide forest management, it is essential to know the relative importance of different types of food and cover in influencing the home range and density of deer, and how the impact of deer relates to variations in forest structure.

4. Current research

We need answers to the following questions:

a) What densities of deer can be tolerated on particular site types for given management objectives?

b) What factors affect these densities?

c) What are the deer's behavioural patterns and food preferences?

d) What are the responses of different plant species and communities to different grazing pressures?

Each of these questions may require many years of fundamental research and to alleviate immediate and pressing problems there is a need for *ad hoc* studies. The Forestry Commission, Red Deer Commission and ITE have recently formed a joint working party to consider the red deer problem in woodlands and evolve an appropriate research programme (Table 50). ITE is making fundamental investigations of grazing to support short- and long-term management studies being initiated by the Forestry Commission and the Red Deer Commission.

ITE has 2 lines of research: the first deals with techniques for estimating numbers or trends in deer populations (Mitchell, project 528). Without the ability to estimate numbers fairly precisely, it will be impossible to execute a rigorous and rational culling programme—existing methods leave much to be desired. The efficiency and accuracy of different counting techniques will be compared, and those based on systematic observations, and on 'drive' and faecal-pellet counts, seem likely to be the most useful. In the second project, the impact and behaviour of resident red deer within a mixed-age Sitka spruce plantation are being studied (Staines & Welch, project 479). Glenbranter Forest, Argyll, has been chosen for this study as it has a mosaic of habitats, with areas of second-rotation plantings next to existing thicket and high forest—a mixture which will be increasingly typical of productive woodland in Britain. The use of different structural types by red and roe deer, and amounts of bark-stripping and browsing on individually marked trees in permanent plots are being monitored, and the performance of the trees affected will be examined subsequently. Feeding behaviour and food preferences, and the home range and movement patterns of individually identified deer are also being investigated. In the long term, we hope to be able to predict the use made by deer of different areas within plantations, integrating their effects on individual trees and on populations.

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Viruses of trees

33. VIRUSES OF TREES

J.I. COOPER and M.L. EDWARDS

1. Perspective

Virus associated diseases are known in more than 40 genera of woody perennials hardy in the United Kingdom (Cooper, 1979) but relatively little is known of their importance except in fruit trees. Knowledge that apple mosaic virus can halve the extension growth of apple trees and decrease girth increments by one fifth suggests, however, that other viruses may threaten amenity trees and production forestry. Although viruses have been detected in the roots of economically important conifers, they have not been detected in their foliage although they are commonly found in that of broadleaved trees. Building on studies of fruit tree viruses made at many institutions, detailed investigations of broadleaved woodland and amenity trees were initiated hoping that the techniques evolved would facilitate the study of viruses in conifers whose detection may have been impeded by copious amounts of resins and related substances. This study was started in 1972 and has been done with the notable collaboration of Dr J.B. Sweet at Long Ashton Research Station.

Following the identification of cherry leaf roll virus (CLRV) in *Betula* spp in UK (Cooper & Atkinson, 1975), effects of the virus on the competitive and regenerative capabilities of birch have been studied. At an early stage, it was observed that seedlings from infected seed, although without foliar discoloration, tended to grow somewhat more slowly than virus-free plants from the same parents (Cooper, 1976*b*).

By comparing pollen from 6 virus-infected and 6 healthy trees it was found that CLRV did not consistently alter percentage germination or rates of pollen tube growth. During a 2-year period following pollination with virus infected pollen, none of the 12 recipient trees *(B. pendula)* became infected; however, some of their seeds were infected. Like *B. pendula,* none of 28 specimens of *Prunus avium* became systematically infected after being pollinated with CLRV-carrying birch pollen. It seems therefore that pollen is not a vehicle of CLRV spread between mature trees of different genera, but further confirmatory evidence is required. However, the evidence to hand is not incompatible with the known properties of cherry leaf roll virus particles, namely that isolates of CLRV from different host genera are serologically distinguishable. CLRV has also been investigated in species of *Juglans.* Although apparently absent from 230 plants of black walnut, *J. nigra,* it was found in 23 of 33 mature specimens of common walnut, *J. regia,* and in 32 of 1046 imported seedlings. As in birch, CLRV has been found to be transmitted in one seed batch of *J. regia* at a rate of 18 in 300 seed.

When assessing the importance of hedgerows as virus reservoirs, *Fraxinus* spp were examined knowing that ash dieback, a debilitating disease with progressive defoliation culminating in death, commonly afflicts virus-infected ash in North America, (Hibben, 1966, 1973; Lana & Agrios, 1974). In UK, where dieback is prevalent, (Figure 59), arabis mosaic virus (AMV) naturally infects *Fraxinus excelsior* (Cooper 1975, 1976*a*) and *F. americana* (Cooper & Sweet, 1976). However,

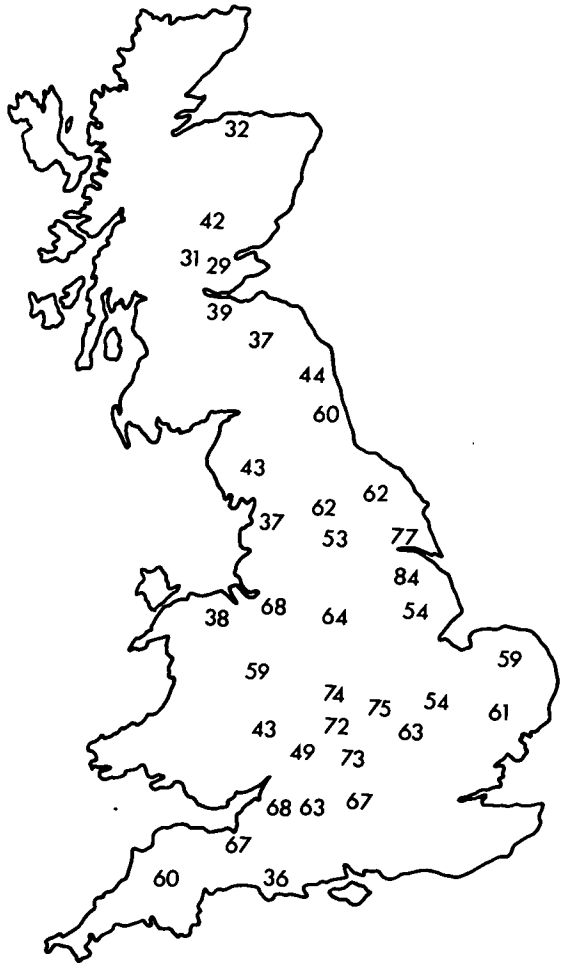

Fig. 59 *Frequency of ash dieback (trees with 10% or more branches from which leaves were absent except at the tips) recorded as a percentage of totals examined in each of 36 counties/metropolitan districts.*

tests made on more than 300 trees showed that dieback was not critically associated with the occurrence of AMV, a deduction supported by the occurrence of ash dieback in regions of Scotland where soils are not infested with the nematode vector of AMV (Taylor & Brown, 1976). Notwithstanding, tests are in progress to assess the long-term effects of AMV on ash in urban localities where its effects may be exacerbated by environmental stresses.

Following Atanasoff's (1935) description of leaf symptoms in poplar, the pathology of the casual virus, poplar mosaic (PMV) has been studied in the Netherlands (Berg, 1964) and in UK (Mackay & Beaton, 1969) where it was thought to decrease growth of *P. x euramericana* clones such as Gelrica, by 25%. However, for this type of work it is desirable to have access to virus-free planting stocks. These have been obtained, using techniques developed for producing virus-free fruit trees. With J.B. Sweet, of Long Ashton Research Station, 9 clones without poplar mosaic virus were produced. One of these (Lons), unlike many others, develops obvious leaf symptoms when infected. For this reason it is now being vegetatively reproduced to enable damage assessments and other types of experiment to be done, including assessments of spread. However tests started in 1975, located at 3 sites and using clones Robusta, Regenerata and I-78, suggest that PMV, if it spreads from tree to tree, does so very slowly, a result justifying the planting of virus-free poplars at least in the UK where it is concluded that vegetative propagation is the most important and possibly the only means of spreading PMV. With R. Koster of Rijksinstituut, De Dorschkamp, and using virus-infected and virus-free *P. nigra* and *P. deltoides* it was found that poplar mosaic virus was not spread in seed or pollen.

The distribution of poplar mosaic virus-like particles and the general ultrastructural appearance of naturally infected poplar foliage (Atkinson & Cooper, 1976) closely resembles that attributed to potato virus M (a carlavirus) in *Phaseolus vulgaris* (Tu & Hiruki, 1971). However, unlike many carla viruses, PMV is not transmitted by species of aphids and mites. Until recently bioassays measuring, albeit inconsistently, the infectivity of leaf extracts by the production of foliar symptoms in test plants were the only way of detecting poplar mosaic virus. Now, however, virus can be detected in frozen poplar leaves (hitherto the inoculum needed to be fresh) using an enzyme-linked immunosorbent assay. It has been possible to confirm that virus concentrations are largest in leaves with severe symptoms. Typically, the oldest leaves which expand in cool weather during the spring are least affected and have the smallest concentrations of virus. The middle leaves of the current year's growth are usually the most severely diseased with the largest concentrations of viruses. The tip leaves become increasingly diseased with the passage of time—a pattern of symptom development that seems common in trees but which requires substantiation and explanation. Virus detection has additionally been improved in other ways. Thus the addition of 1% nicotine, 3.5% polyvinyl pyrolidone (MW 44000)), 0.1% thioglycerol and 0.02 m diethyl dithocarbamate to phosphate buffer increased by a factor of x 1000 the quantities of CLRV extracted from leaves of *Juglans regia.*

2. The way ahead

Added to the observations made by fruit tree virologists, results already obtained emphasize the widespread occurrence of viruses in trees of all sorts. However, our knowledge is scant. In particular, virtually nothing is known of the significance of viruses in woodland and amenity trees. Are they damaging and, if so, to what extent? Are they a threat to other types of plant? To this end, growth rate studies are being made with cherry leaf roll virus and birch; arabis mosaic virus and ash; and poplar mosaic virus and poplar; 3 model systems which will be kept under surveillance for long periods to investigate whether viruses diminish host vigour at constant rates or whether tree growth is, but temporarily, checked following infection.

Cherry leaf roll virus seems to have a predilection for perennial woody hosts yet little is known about its biology. Curiously it can be transmitted from infected pollen to seed but not to the mother plant—why? Why are most specimens of common walnut in southern England (albeit of a small sample) infected when fewer than 10% of seed carry the virus? Is the virus like others, transmitted in a variety of ways? What are these? To enable these questions to be answered effectively it is necessary to sustain work on virus characterization, enabling their separation and identification. In a small survey made of *J. regia,* more than 30 virus isolates were obtained. Are they all the same? Are the differences among them biologically significant? How should these be characterized? Increasingly virologists resort to a blend of physico-chemical and biological methods so as to gain insight into the ways in which viruses vary, relating chemical constitution to infectivity and serological properties.

The environments in which viruses exist are multidimensional. Viruses depend upon their vectors; they are influenced by the susceptibility and tolerance of their different hosts which in turn are likely to change at different stages of development and at different seasons. It must be recognised that

the genetical variation within a single species population of plants is likely to be matched by comparable variation within viruses. In summary, the role of viruses in trees is a complex picture but one in which preliminary observations on woodland and amenity trees suggest that further work is needed, the amount of commitment being determined to a considerable extent by the hazard posed to plant growth and hence the ability of plants to compete with others.

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LISTS OF COMMON NAMES AND LATIN BINOMIALS

In preparing lists for:

1. CRYPTOGAMS
2. SPERMATOPHYTES
3. INVERTEBRATES

and 4. VERTEBRATES

the following sources were consulted:

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1. CRYPTOGAMS

A. Latin binomial to common name.

Amanita muscaria	Fly agaric
Ceratocystis fagacearum	Oak wilt pathogen
Ceratocystis ulmi	Dutch elm disease pathogen
Dryopteris dilatata	Broad buckler-fern
Hebeloma crustuliniforme	Fairy-cake mushroom
Hebeloma spp	
Inocybe spp	
Laccaria laccata	Deceiver
Laccaria spp	
Lactarius pubescens	
Leccinum spp	
Leucobryum glaucum	
Mycosyrinx spp	
Odontoschisma sphagni	
Paxillus involutus	Brown roll-rim
Pleurozium schreberi	
Polytrichum formosum	
Pteridium aquilinum	Bracken
Rhizobium trifolii	
Scleroderma spp	
Sphagnum palustre	

B. Common name to Latin binomial.

Bracken	*Pteridium aquilinum*
Broad buckler-fern	*Dryopteris dilatata*
Brown roll-rim	*Paxillus involutus*
Deceiver	*Laccaria laccata*

Dutch elm disease pathogen	*Ceratocystis ulmi*
Fairy-cake mushroom	*Hebeloma crustuliniforme*
Fly agaric	*Amanita muscaria*
Oak wilt pathogen	*Ceratocystis fagacearum*

2. SPERMATOPHYTES

A. Latin binomial to common name.

Abies alba	Common silver fir
Abies grandis	Grand fir
Abies spp	Silver fir
Acer campestre	Field or Common maple
Acer platanoides	Norway maple
Acer pseudoplatanus	Sycamore
Acer saccharum	Sugar maple
Acer tartaricum	Tartar maple
Aesculus hippocastanum	Horse-chestnut
Agrostis canina	Brown bent
Agrostis spp	Bent
Agrostis stolonifera	Creeping bent
Agrostis tenuis	Common bent
Ajuga reptans	Bugle
Alnus glutinosa	Common alder
Alnus incana	Grey alder
Andromeda polifolia	Marsh Andromeda
Anemone nemorosa	Wood anemone
Anthoxanthum odoratum	Sweet vernal grass
Betula pendula (B. verrucosa)	Silver birch
Betula pubescens	Downy birch
Betula pubescens ssp *carpatica*	
Betula pubescens ssp *odorata*	
Betula pubescens ssp *tortuosa*	
Buxus sempervirens	Box
Calluna vulgaris	Heather
Carex pallescens	Pale sedge
Carex pendula	Pendulous sedge
Carex remota	Remote sedge
Carex sylvatica	Wood sedge
Carpinus betulus	Hornbeam
Castanea sativa	Sweet chestnut
Cedrus spp	Cedar
Centaurium erythraea	Common centaury
Chamaecyparis nootkatensis	Nootka cypress
Chenopodium album	Fat hen
Cirsium palustre	Marsh thistle
Cordia alliodora	American light cordia
Corydalis claviculata	White climbing fumitory
Corylus avellana	Hazel or cobnut
Cotoneaster spp	Cotoneaster
Crataegus monogyna	Hawthorn
Cupressus arizonica	Rough-barked Arizona cypress
Cupressus macrocarpa	Monterey cypress
Deschampsia cespitosa	Tufted hair-grass
Deschampsia flexuosa	Wavy hair-grass
Digitalis purpurea	Foxglove
Endymion non-scriptus	Bluebell
Epilobium adenocaulon	American willow-herb
Erica tetralix	Cross-leaved heath
Eriophorum angustifolium	Common cottongrass

Eriophorum vaginatum	Hare's-tail cotton-grass
Euphorbia amygdaloides	Wood spurge
Fagus orientalis	Oriental beech
Fagus sylvatica	Common beech
Festuca spp	Fescue
Fragaria vesca	Wild strawberry
Frangula alnus	Alder buckthorn
Fraxinus americana	White ash
Fraxinus excelsior	Common ash
Fraxinus ornus	Manna or Flowering ash
Gnaphalium uliginosum	Marsh cudweed
Hepatica nobilis	Hepatica
Holcus lanatus	Yorkshire fog
Hypericum hirsutum	Hairy St. John's wort
Hypericum humifusum	Trailing St. John's wort
Hypericum pulchrum	Slender St. John's wort
Hypericum tetrapterum	Square-stemmed St. John's wort
Ilex aquifolium	Holly
Iris pseudacorus	Yellow flag
Isolepis setacea	Bristle scirpus
Juglans nigra	Black walnut
Juglans regia	Common walnut
Juncus bufonius	Toad rush
Juncus effusus	Soft rush
Juniperus communis	Juniper
Laburnum anagyroides	Laburnum
Lamiastrum galeobdolon	Yellow archangel
Larix decidua	European larch
Larix kaempferi	Japanese larch
Larix x eurolepis	Dunkeld hybrid larch
Lathyrus pratensis	Meadow vetchling
Lonicera periclymenum	Honeysuckle
Lotus corniculatus	Bird's-foot-trefoil
Lupinus spp	Lupin
Luzula pilosa	Hairy woodrush
Luzula sylvatica	Greater woodrush
Lysimachia nemorum	Yellow pimpernel
Malus spp	Apple
Mercurialis perennis	Dog's mercury
Moehringia trinervia	Three-nerved sandwort
Molinia caerulea	Purple moor-grass
Nothofagus obliqua	Roble beech
Nothofagus procera	Raoul
Oxalis acetosella	Wood-sorrel
Phalaris arundinacea	Reed-grass
Picea abies	Norway spruce
Picea sitchensis	Sitka spruce
Pinus contorta	Lodgepole, Beach or Shore pine
Pinus mugo	Mountain pine
Pinus nigra var *maritima*	Corsican pine
Pinus pseudostrobus	
Pinus sylvestris	Scots pine
Pinus taeda	Loblolly pine
Plantago major	Great plantain
Poa nemoralis	Wood poa
Poa trivialis	Rough meadow-grass
Polygonum aviculare	Knotgrass
Polygonum convolvulus	Black bindweed
Polygonum lapathifolium	Pale persicaria
Polygonum persicaria	Persicaria
Populus deltoides	Eastern cottonwood

Populus nigra	Black poplar
Populus tremula	Aspen
Populus x euramericana	Hybrid black poplar
Potentilla erecta	Common Tormentil
Potentilla sterilis	Barren strawberry
Primula vulgaris	Primrose
Prunella vulgaris	Selfheal
Prunus avium	Wild cherry or Gean
Prunus serotina	Black cherry
Prunus spinosa	Blackthorn
Pseudotsuga menziesii	Douglas fir
Quercus borealis (Q. rubra)	Red oak
Quercus cerris	Turkey oak
Quercus ilex	Evergreen oak
Quercus petraea	Sessile or Durmast oak
Quercus pubescens	Downy oak
Quercus robur	Pedunculate or Common oak
Ranunculus acris	Meadow buttercup
Ranunculus flammula	Lesser spearwort
Ranunculus repens	Creeping buttercup
Raphanus spp	Radish
Rhododendron ponticum	Rhododendron
Rosa spp	Rose
Rubus caesius	Dewberry
Rubus fruticosus	Bramble or Blackberry
Rumex acetosa	Sorrel
Rumex acetosella	Sheep's sorrel
Rumex obtusifolius	Broad-leaved dock
Sagina procumbens	Procumbent pearlwort
Salix caprea	Goat or Great willow
Salix spp	Willow
Sambucus nigra	Elder
Sambucus racemosa	Red-berried elder
Sarothamnus scoparius	Broom
Scrophularia nodosa	Common figwort
Senecio vulgaris	Groundsel
Silene dioica	Red campion
Solanum nigrum	Black nightshade
Solidago virgaurea	Golden-rod
Sorbus aucuparia	Rowan or Mountain ash
Stachys sylvatica	Hedge woundwort
Stellaria media	Chickweed
Syringa vulgaris	Lilac
Thuja plicata	Western red cedar
Tilia cordata	Small-leaved lime
Tilia spp	Lime
Trichophorum cespitosum	Deer-grass
Trifolium repens	White clover
Tripleurospermum maritimum inodorum	Scentless mayweed
Triplochiton scleroxylon	Obeche
Tsuga spp	Hemlock
Ulmus carpinifolia	Small-leaved elm
Ulmus glabra	Wych elm
Ulmus spp	Elm
Vaccinium myrtillus	Bilberry or Whortleberry
Vaccinium oxycoccos	Cranberry
Vaccinium vitis-idaea	Cowberry
Veronica chamaedrys	Germander speedwell
Veronica montana	Wood speedwell
Veronica serpyllifolia	Thyme-leaved speedwell
Viola riviniana	Common violet
x Cupressocyparis leylandii	Leyland cypress

B. Common name to Latin binomial.

Alder buckthorn	*Frangula alnus*
American light cordia	*Cordia alliodora*
American willow-herb	*Epilobium adenocaulon*
Apple	*Malus* spp
Aspen	*Populus tremula*
Barren strawberry	*Potentilla sterilis*
Bent	*Agrostis* spp
Bilberry or Whortleberry	*Vaccinium myrtillus*
Bird's-foot-trefoil	*Lotus corniculatus*
Black bindweed	*Polygonum convolvulus*
Black cherry	*Prunus serotina*
Black nightshade	*Solanum nigrum*
Black poplar	*Populus nigra*
Black walnut	*Juglans nigra*
Blackthorn	*Prunus spinosa*
Bluebell	*Endymion non-scriptus*
Box	*Buxus sempervirens*
Bramble or Blackberry	*Rubus fruticosus*
Bristle scirpus	*Isolepis setacea*
Broad-leaved dock	*Rumex obtusifolius*
Broom	*Sarothamnus scoparius*
Brown bent	*Agrostis canina*
Bugle	*Ajuga reptans*
Cedar	*Cedrus* spp
Chickweed	*Stellaria media*
Common alder	*Alnus glutinosa*
Common ash	*Fraxinus excelsior*
Common beech	*Fagus sylvatica*
Common bent	*Agrostis tenuis*
Common centaury	*Centaurium erythraea*
Common cottongrass	*Eriophorum angustifolium*
Common figwort	*Scrophularia nodosa*
Common silver fir	*Abies alba*
Common tormetil	*Potentilla erecta*
Common violet	*Viola riviniana*
Common walnut	*Juglans regia*
Corsican pine	*Pinus nigra* var *maritima*
Cotoneaster	*Cotoneaster* spp
Cowberry	*Vaccinium vitis-idaea*
Cranberry	*Vaccinium oxycoccos*
Creeping bent	*Agrostis stolonifera*
Creeping buttercup	*Ranunculus repens*
Cross-leaved heath	*Erica tetralix*
Deer-grass	*Trichophorum cespitosum*
Dewberry	*Rubus caesius*
Dog's mercury	*Mercurialis perennis*
Douglas fir	*Pseudotsuga menziesii*
Downy birch	*Betula pubescens*
Downy oak	*Quercus pubescens*
Dunkeld hybrid larch	*Larix x eurolepis*
Eastern cottonwood	*Populus deltoides*
Elder	*Sambucus nigra*
Elm	*Ulmus* spp
European larch	*Larix decidua*
Fat hen	*Chenopodium album*
Fescue	*Festuca* spp
Field or Common maple	*Acer campestre*
Foxglove	*Digitalis purpurea*
Germander speedwell	*Veronica chamaedrus*

Goat or Great willow	*Salix caprea*
Golden-rod	*Solidago virgaurea*
Grand fir	*Abies grandis*
Great plantain	*Plantago major*
Greater woodrush	*Luzula sylvatica*
Grey alder	*Alnus incana*
Groundsel	*Senecio vulgaris*
Hairy St. John's wort	*Hypericum hirsutum*
Hairy woodrush	*Luzula pilosa*
Hare's-tail cotton-grass	*Eriophorum vaginatum*
Hawthorn	*Crataegus monogyna*
Hazel or Cobnut	*Corylus avellana*
Heather	*Calluna vulgaris*
Hedge woundwort	*Stachys sylvatica*
Hemlock	*Tsuga* spp
Hepatica	*Hepatica nobilis*
Holly	*Ilex aquifolium*
Holm oak	*Quercus ilex*
Honeysuckle	*Lonicera periclymenum*
Hornbeam	*Carpinus betulus*
Horse-chestnut	*Aesculus hippocastanum*
Hybrid black poplar	*Populus x euramericana*
Japanese larch	*Larix kaempferi*
Juniper	*Juniperus communis*
Knotgrass	*Polygonum aviculare*
Laburnum	*Laburnum anagyroides*
Lesser spearwort	*Ranunculus flammula*
Leyland cypress	*x Cupressocyparis leylandii*
Lilac	*Syringa vulgaris*
Lime	*Tilia* spp
Loblolly pine	*Pinus taeda*
Lodgepole, Beach or Shore pine	*Pinus contorta*
Lupin	*Lupinus* spp
Manna or flowering ash	*Fraxinus ornus*
Marsh Andromeda	*Andromeda polifolia*
Marsh cudweed	*Gnaphalium uliginosum*
Marsh thistle	*Cirsium palustre*
Meadow buttercup	*Ranunculus acris*
Meadow vetchling	*Lathyrus pratensis*
Monterey cypress	*Cupressus macrocarpa*
Mountain pine	*Pinus mugo*
Nootka cypress	*Chamaecyparis nootkatensis*
Norway maple	*Acer platanoides*
Norway spruce	*Picea abies*
Obeche	*Triplochiton scleroxylon*
Oriental beech	*Fagus orientalis*
Pale persicaria	*Polygonum lapathifolium*
Pale sedge	*Carex pallescens*
Pedunculate or Common oak	*Quercus robur*
Pendulous sedge	*Carex pendula*
Persicaria	*Polygunum persicaria*
Primrose	*Primula vulgaris*
Procumbent pearlwort	*Sagina procumbens*
Purple moor-grass	*Molinia caerulea*
Radish	*Raphanus* spp
Raoul	*Nothofagus procera*
Red campion	*Silene dioica*
Red oak	*Quercus borealis (Q. rubra)*
Red-berried elder	*Sambucus racemosa*
Reed-grass	*Phalaris arundinacea*
Remote sedge	*Carex remota*

Rhododendron	*Rhododendron ponticum*
Roble beech	*Nothofagus obliqua*
Rose	*Rosa* spp
Rough meadow-grass	*Poa trivialis*
Rough-barked Arizona cypress	*Cupressus arizonica*
Rowan or Mountain ash	*Sorbus aucuparia*
Scentless mayweed	*Tripleurospermum maritimum inodorum*
Scots pine	*Pinus sylvestris*
Selfheal	*Prunella vulgaris*
Sessile or Durmast oak	*Quercus petraea*
Sheep's sorrel	*Rumex acetosella*
Silver birch	*Betula pendula (B. verrucosa)*
Silver fir	*Abies* spp
Sitka spruce	*Picea sitchensis*
Slender St. John's wort	*Hypericum pulchrum*
Small-leaved elm	*Ulmus carpinifolia*
Small-leaved lime	*Tilia cordata*
Soft rush	*Juncus effusus*
Sorrel	*Rumex acetosa*
Square-stemmed St. John's wort	*Hypericum tetrapterum*
Sugar maple	*Acer saccharum*
Sweet chestnut	*Castanea sativa*
Sweet vernal grass	*Anthoxanthum odoratum*
Sycamore	*Acer pseudoplatanus*
Tartar maple	*Acer tartaricum*
Three-nerved sandwort	*Moehringia trinervia*
Thyme-leaved speedwell	*Veronica serpyllifolia*
Toad rush	*Juncus bufonius*
Trailing St. John's wort	*Hypericum humifusum*
Tufted hair-grass	*Deschampsia cespitosa*
Turkey oak	*Quercus cerris*
Wavy hair-grass	*Deschampsia flexuosa*
Western red cedar	*Thuja plicata*
White ash	*Fraxinus americana*
White climbing fumitory	*Corydalis claviculata*
White clover	*Trifolium repens*
Wild cherry or Gean	*Prunus avium*
Wild strawberry	*Fragaria vesca*
Willow	*Salix* spp
Wood anemone	*Anemone nemorosa*
Wood poa	*Poa nemoralis*
Wood sedge	*Carex sylvatica*
Wood speedwell	*Veronica montana*
Wood spurge	*Euphorbia amygdaloides*
Wood-sorrel	*Oxalis acetosella*
Wych elm	*Ulmus glabra*
Yellow archangel	*Lamiastrum galeobdolon*
Yellow flag	*Iris pseudacorus*
Yellow pimpernel	*Lysimachia nemorum*
Yorkshire fog	*Holcus lanatus*

3. INVERTEBRATES

A. Latin binomial to common name.

Abraeus granulum	
Acronicta psi	Grey dagger
Adalia 10-punctata	
Adalia bipunctata	
Agriopis asurantiaria	Scarce umber

Agriopis marginaria	Dotted border
Allolobophoera spp	
Ampedus cardinalis	
Anaspis rufilabris	
Anatis ocellata	
Aphidecta obliterata	
Apion spp	
Apocheima hispidaria	Small brindled beauty
Apocheima pilosaria	Pale brindled beauty
Argynnis adippe	High-brown fritillary
Argynnis paphia	Silver-washed fritillary
Biston betularia	Peppered moth
Biston strataria	Oak beauty
Bitoma crenata	
Boloria euphrosyne	Pearl-bordered fritillary
Boloria selene	Small pearl-bordered fritillary
Brachionycha sphinx	Sprawler
Brachypterus urticae	
Calvia 14-guttata	
Cantharis decipiens	
Cantharis nigricans	
Carcina quercana	
Coccinella 7-punctata	
Coeliodes dryados	
Colocasia coryli	Nut-tree tussock
Cortinicara gibbosa	
Crocallis elinguaria	Scalloped oak
Curculio pyrrhoceras	
Dalopius marginatus	
Denticollis linearis	
Deporaus betulae	
Dryophilus pusillus	
Ectropis bistortata	Engrailed
Eilema deplana	Buff footman
Enicmus transversus	
Ennomos erosaria	September thorn
Epirrita autumnata	Autumnal moth
Errannis defoliaria	Mottled umber
Euproctis similis	Yellow-tail
Exochomus 4-pustulatus	
Ischnomera sanguinicollis	
Ladoga camilla	White admiral
Leptidea sinapis	Wood white
Litargus connexus	
Lumbricus rubellus	
Lumbricus terrestris	
Lymantria monacha	Black archer
Malthodes marginatus	
Operophtera brumata	Winter moth
Orgyia antiqua	Vapourer
Orthosia cruda	Small quaker
Orthosia gothica	Hebrew character
Orthosia stabilis	Common quaker
Otiorhynchus rugosostriatus	
Pandemis corylana	Chequered fruit-tree tortrix
Pandemis heparana	Dark fruit-tree tortrix
Pararge aegeria	Speckled wood
Pediacus dermestoides	
Phalera bucephala	Buff-tip
Phloiotrya vaudoueri	
Phyllobius argentatus	

Polydrusus cervinus	
Pseudopityophthorus spp	
Ptenidium gressneri	
Rhagonycha lignosa	
Rhinosimus planirostris	
Rhizophagus oblongicollis	
Rhynchaenus avellanae	
Rhynchaenus quercus	
Scolytus intricatus	Oak bark-beetle
Scolytus multistriatus	Small elm bark-beetle
Scolytus scolytus	Large elm bark-beetle
Scymnus suturalis	
Stilbus testaceus	
Strophosomus capitatus	
Strophosomus melanogrammus	
Strymonidia pruni	Black hairstreak

3. Common name to Latin binomial.

Autumnal moth	*Epirrita autumnata*
Black archer	*Lymantria monacha*
Black hairstreak	*Strymonidia pruni*
Buff footman	*Eilema deplana*
Buff-tip	*Phalera bucephala*
Chequered fruit-tree tortrix	*Pandemis corylana*
Common quaker	*Orthosia stabilis*
Dark fruit-tree tortrix	*Pandemis heparana*
Dotted border	*Agriopis marginaria*
Engrailed	*Ectropis bistortata*
Grey dagger	*Acronicta psi*
Hebrew character	*Orthosia gothica*
High-brown fritillary	*Argynnis adippe*
Large elm bark-beetle	*Scolytus scolytus*
Mottled umber	*Errannis defoliaria*
Nut-tree tussock	*Colocasia coryli*
Oak bark-beetle	*Scolytus intricatus*
Oak beauty	*Biston strataria*
Pale brindled beauty	*Apocheima pilosaria*
Pearl-bordered fritillary	*Bolaria euphrosyne*
Peppered moth	*Biston betularia*
Scalloped oak	*Crocallis elinguaria*
Scarce umber	*Agriopis asurantiaria*
September thorn	*Ennomos erosaria*
Silver-washed fritillary	*Argynnis paphia*
Small brindled beauty	*Apocheima hispidaria*
Small elm bark-beetle	*Scolytus multistriatus*
Small pearl-bordered fritillary	*Boloria selene*
Small quaker	*Orthosia cruda*
Speckled wood	*Pararge aegeria*
Sprawler	*Brachionycha sphinx*
Vapourer	*Orgyia antiqua*
White admiral	*Ladoga camilla*
Winter moth	*Operophtera brumata*
Wood white	*Leptidea sinapis*
Yellow-tail	*Euproctis similis*

4. VERTEBRATES

A. Latin binomial to common name.

Accipiter nisus	Sparrowhawk

Aegithalos caudatus	Long-tailed tit
Alauda arvensis	Skylark
Anthus pratensis	Meadow pipit
Anthus trivialis	Tree pipit
Asio flammeus	Short-eared owl
Asio otus	Long-eared owl
Capreolus capreolus	Roe deer
Carduelis chloris	Greenfinch
Carduelis flammea	Redpoll
Carduelis spinus	Siskin
Certhia familiaris	Tree creeper
Cervus elaphus	Red deer
Cervus nippon	Sika deer
Cinclus cinclus	Dipper
Clerthrionomys glareolus	Bank vole
Columba palumbus	Wood pigeon
Corvus corax	Raven
Corvus corone	Carrion crow
Cuculus canorus	Cuckoo
Dama dama	Fallow deer
Dendroconus major	Great spotted woodpecker
Emberiza citrinella	Yellowhammer
Emberiza schoeniclus	Reed bunting
Erithacus rubecula	Robin
Falco columbarius	Merlin
Falco tinnunculus	Kestrel
Garrulus glandarius	Jay
Hydropotes inermis	Chinese water deer
Locustella naevia	Grasshopper warbler
Loxia curvirostra	Crossbill
Lyrurus tetrix	Black grouse
Mergus merganser	Goosander
Microtus agrestis	Field vole
Muscicapa striata	Spotted flycatcher
Mustela erminea	Stoat
Mustela nivalis	Weasel
Numernius arquata	Curlew
Oenanthe oenanthe	Wheatear
Parus ater	Coal tit
Parus montanus	Willow tit
Parus caeruleus	Blue tit
Parus cristatus	Crested tit
Parus major	Great tit
Phoenicurus phoenicurus	Redstart
Phylloscopus trochilus	Willow warbler
Prunella modularis	Dunnock
Pyrrhula pyrrhula	Bullfinch
Regulus regulus	Goldcrest
Saxicola rubetra	Whinchat
Saxicola torquata	Stonechat
Sciurus carolinensis	Grey squirrel
Sciurus niger	Fox squirrel
Sciurus vulgaris	Red squirrel
Scolopax rusticola	Woodcock
Strix aluco	Tawny owl
Sturnus vulgaris	Starling
Sylvia atricapilla	Blackcap
Sylvia communis	Whitethroat
Troglodytes troglodytes	Wren
Turdus merula	Blackbird
Turdus philomelos	Song thrush

Turdus viscivorus	Mistle thrush
Tyto alba	Barn owl
Vulpes vulpes	Red fox

B. Common name to Latin binomial.

Bank vole	*Clerthrionomys glareolus*
Barn owl	*Tyto alba*
Black grouse	*Lyrurus tetrix*
Blackbird	*Turdus merula*
Blackcap	*Sylvia atricapilla*
Blue tit	*Parus caeruleus*
Bullfinch	*Pyrrhula pyrrhula*
Carrion crow	*Corvus corone*
Chinese water deer	*Hydropotes inermis*
Coal tit	*Parus ater*
Crested tit	*Parus cristatus*
Crossbill	*Loxia curvirostra*
Cuckoo	*Cuculus canorus*
Curlew	*Numernius arquata*
Dipper	*Cinclus cinclus*
Dunnock	*Prunella modularis*
Fallow deer	*Dama dama*
Field vole	*Microtus agrestis*
Fox squirrel	*Sciurus niger*
Goldcrest	*Regulus regulus*
Goosander	*Mergus merganser*
Grasshopper warbler	*Locustella naevia*
Great spotted woodpecker	*Dendroconus major*
Great tit	*Parus major*
Greenfinch	*Carduelis chloris*
Grey squirrel	*Sciurus carolinensis*
Jay	*Garrulus glandarius*
Kestrel	*Falco tinnunculus*
Long-eared owl	*Asio otus*
Long-tailed tit	*Aegithalos caudatus*
Meadow pipit	*Anthus pratensis*
Merlin	*Falco columbarius*
Mistle thrush	*Turdus viscivorus*
Raven	*Corvus corax*
Red deer	*Cervus elaphus*
Red fox	*Vulpes vulpes*
Red squirrel	*Sciurus vulgaris*
Redpoll	*Carduelis flammea*
Redstart	*Phoenicurus phoenicurus*
Reed bunting	*Emberiza schoeniclus*
Robin	*Erithacus rubecula*
Roe deer	*Capreolus capreolus*
Short-eared owl	*Asio flammeus*
Sika deer	*Cervus nippon*
Siskin	*Carduelis spinus*
Skylark	*Alauda arvensis*
Song thrush	*Turdus philomelos*
Sparrowhawk	*Accipiter nisus*
Spotted flycatcher	*Muscicapa striata*
Starling	*Sturnus vulgaris*
Stoat	*Mustela erminea*
Stonechat	*Saxicola torquata*
Tawny owl	*Strix aluco*
Tree creeper	*Certhia familiaris*
Tree pipit	*Anthus trivialis*

Weasel	*Mustela nivalis*
Wheatear	*Oenanthe oenanthe*
Whinchat	*Saxicola rubetra*
Whitethroat	*Sylvia communis*
Willow tit	*Parus montanus*
Willow warbler	*Phylloscopus trochilus*
Wood pigeon	*Columba palumbus*
Woodcock	*Scolopax rusticola*
Wren	*Troglodytes troglodytes*
Yellowhammer	*Emberiza citrinella*

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